REVISIONS OF MALLOPHAGA GENERA. *DEGEERIELLA* FROM THE FALCONIFORMES

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REVISIONS OF MALLOPHAGA GENERA. *DEGEERIELLA* FROM THE FALCONIFORMES

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INTRODUCTION

Before attempting to define the genus *Degeeriella*, the type species of which parasitizes one of the Falconiformes, it is necessary to consider shortly the whole of the *Degeeriella*-complex.

The *Degeeriella*-complex. It is difficult to delimit this group exactly but the following genera should probably be included : *Degeeriella* Neumann (= *Kélerinirmus* Eichler), *Acutifrons* Guimarães, *Austrophilopterus* Ewing, *Capraiella* Conci, *Cotingacola* Carriker, *Cuculicola* Clay & Meinertzhagen, *Lagopecus* Waterston (= *Colinicola* Carriker), *Picicola* Clay & Meinertzhagen (= *Tyrannicola* Carriker), *Trogoninirmus* Eichler, *Upupicola* Clay & Meinertzhagen, a group of undescribed species from the Bucerotidae, and an undescribed species from the Megapodidae, probably an aberrant *Lagopecus*. *Buceronirmus* Hopkins and *Hopkinsiella* Clay & Meinertzhagen should also perhaps be included here. Possible derivatives from this group include *Syrrhaptoecus* Waterston, *Tinamotaecola* Carriker, some of the Ischnocera from the Bucerotidae and also possibly *Penenirmus*. The complex (omitting the doubtful members) can be defined as follows :

Ischnocera with marginal carina of head usually complete dorsally but may be partially interrupted anteriorly, and also partially interrupted each side when a dorsal preantennal suture is present ; ventrally it may be complete or interrupted medially. Hyaline margin absent or small, never greatly enlarged and never continuous with hyaline area delimiting a complete dorsal anterior plate. Ventral carina never forms a semicircular band, but is interrupted medially ; usually the two carinae pass towards the anterior margin of the head but never form well defined bands continuous with the marginal carina, and only rarely have the strongly sclerotized parallel surfaces to which are attached lobes of the pulvinus as in *Brüelia* (Clay, 1951) ; pulvinus usually in the form of a single sac-like structure.[1] Ocular seta (except in *Trogoninirmus* and *Austrophilopterus*) and at least two of the temporal

[1] At one time it was thought possible to use the characters of the ventral carinae and pulvinus to separate the *Degeeriella*- and *Brüelia*-complexes, however the species of *Degeeriella* from *Chelictina* and *Elanoides* have the characters of these structures as in some species of *Brüelia* (see Clay, 1958).

setae elongated. Prothorax with one marginal seta each side (except in *Lagopoecus meinertzhageni* Clay); third episternum fully sclerotized laterally. Abdomen with postspiracular setae on segments III–VII[1] (exceptionally on IV–V only) with sensillae on III or IV–V. Tergal plates entire or separated medially; sternal plates median, lateral or absent. In the male segments IX–X with a single fused tergal plate (entire or divided medially), separated from XI by a suture and setae; anal and genital openings close together on dorsal surface, dorsal part of XI narrowed with the 3 + 3 anal setae on the dorsal surface of the abdomen (see Clay, 1953). Male genitalia usually with sclerotized penis, short curved parameres, the outer and inner edges of which are continuous with the basal apodeme, and endomeral plate of characteristic form (Pl. 8, fig. 7). This basic form which is found in some species of most of the genera is also found modified to a greater or lesser extent in a few species belonging to many of the genera and in some species the basic degeerielline pattern can no longer be recognized, for instance, there may be an articulation between the parameres and the basal apodeme. The genitalia do not provide good group characters in this complex; these structures in *Acutifrons megalopterus* Carriker and *Degeeriella rufa* (Burmeister) for instance, being more similar to each other than are those of *A. megalopterus* and *A. caracarensis* (Kellogg & Mann); and those of *Capraiella subcuspidata* (Burmeister) are nearer those of *D. fulva* (Giebel) than are those of *D. fulva* and *D. mookerjeei* Clay.

The internal male genitalia are too various, even within one related group (see below, p. 127) to be used as diagnostic characters for the complex, but a general type similar to that of *D. fulva* from *Buteo* (Text-fig. 1) with or without the lateral lobes is found in some of the species of many of the genera; all the species examined with one exception (a *Picicola* from one of the Tyrannidae) have the ductus ejaculatorius long and coiled. An examination has been made of the internal male genitalia of about 150 species belonging to 73 genera of the Ischnocera; it was hoped that the characters of these organs might help in the generic or suprageneric classification of this superfamily. The members of the *Gonides*-complex (including only those found on the Galliformes and Columbidae) have the vesicular apparatus (see further below) formed of two simple lobes, not joined medially and the ductus ejaculatorius modified in some way, they differ in these characters from *Austrogonoides*, *Osculotes*, *Chelopistes* and members of the *Heptapsogaster*-complex. The *Otidoecus*-complex (*Otidoecus*, *Rhynonirmus* and *Cuclotogaster*) have an unpaired diverticulum arising from the ductus ejaculatorius[2]. Apart from these two groups it has not been possible to find characters of generic or suprageneric importance, although they may be of specific or of species group value. Recently Blagoveshtchensky (1956) has published a most useful and extensive account with many figures of the internal genitalia of both Ischnocera and Amblycera.

In the female the genital plate (when present) does not reach to the upper margin of the vulva (cf. *Brüelia*); genital region without lateral spine-like setae (cf. *Rallicola*) or clump of setae on tubercle-like area (cf. *Brüelia*). Inner genital sclerites and

[1] As in previous publications roman numerals are used for the true segments, see below, p. 126.
[2] The presence of this diverticulum and other characters make it certain that the "*Lipeurus variabilis*" in Strindberg, 1918 : 633 was in fact *Cuclotogaster heterographus* (Nitzsch).

subvulval sclerites present (Text-figs. 96, 97). Spermatheca with sclerotized calyx and simple thin-walled sac.

It has not been possible to find any characters separating the females of the *Degeeriella*-complex from those of the *Otidoecus*-complex (i.e. *Cuclotogaster, Otidoecus* and *Rhynonirmus*) except that in the latter the calyx of the spermatheca is never apparent and it has not been possible to find any sign of a spermatheca in dissected specimens (no sections examined). The males are quite distinct : in the *Otidoecus*-complex the genital opening is terminal or ventro-terminal, intertergital sclerites are present and the ductus ejaculatorius has an unpaired diverticulum not yet found elsewhere amongst the Ischnocera.

The present distribution of the *Degeeriella*-complex suggests that an ancestral stock must have been present on birds at an early stage of their evolution and that the Mallophaga have diverged with their hosts. On some host groups there are more than one species group belonging to the *Degeeriella*-complex, these presumably having diverged from each other on the host group in question ; these species groups are either sympatric and probably restricted to different ecological niches on the host, or allopatric and restricted to different taxonomic divisions of the host group. The species belonging to one of these groups have large heads and rounded abdomens with the characters frequently found in this type : that is a dorsal preantennal suture, temporal carinae, pleural thickening less well developed, and the tergites and sternites narrowed or interrupted medially ; the other is the more elongate form as found in *Degeeriella fulva* (Pl. 1, fig. 1). There appears to have been a considerable amount of parallel evolution in the degeerielline stocks resulting in a superficial resemblance between the species groups on different host groups. For instance, an undescribed species of *Lagopoecus* from the Megapodidae, *Acutifrons vierai* Guimarães from the Accipitridae and *Cuculicola acutus* (Rudow) from the Cuculidae all have large heads pointed anteriorly, preantennal dorsal sutures and partial or complete temporal carinae passing posteriorly from the preantennal nodus ; the genitalia are all of the typical degeerielline type or modifications of it. Again *Cuculicola latirostris* from *Cuculus canorus* resembles superficially such species of *Degeeriella* as *D. rufa* from *Falco tinnunculus*, while the *Cuculicola* species from *Geococcyx* resembles *Acutifrons megalopterus* Carriker from a hawk (*Phalcoboenus*) in the broad head and abdomen and the form of the preantennal suture, in both genitalia are of the degeerielline type. In all these cases the species have retained the basic form of the abdominal tergites and sometimes the sternites : the species from the Galliformes have the divided tergal and sternal plates, those from the Falconiformes have the entire tergal and sternal plates, while those from the Cuculidae have the anterior tergal plates at least, divided.

The stability of certain characters and the divergence of the ancestral degeerielline stock on the various host groups together with parallel evolution makes it impossible to define a subfamily for the *Degeeriella*-complex, and further causes great difficulty in generic separation. It is possible with further study based on more material that some of the genera now recognized will have to be re-incorporated in *Degeeriella*.

Degeeriella as found on the Falconiformes is here defined in detail and the characters found throughout the genus will not be repeated in the descriptions of the individual species which follow.

DEGEERIELLA Neumann, 1906

Nirmus. Nitzsch, 1818, *Germar's Mag. Ent.* **3** : 291 (*nec* Hermann, 1804).

Degeeriella. Neumann, 1906, *Bull. Soc. zool. Fr.* **20** : 60. *Nomen novum* for *Nirmus* Nitzsch *nec* Hermann. Type species by subsequent designation, Johnston & Harrison, 1911, *Proc. Linn. Soc. N.S.W.* **36** : 326 : " *D. discocephalus* N."

Kélerinirmus. Eichler, 1940, *Zool. Anz.* **130** : 101. Type species : " *Nirmus fuscus* Nitzsch in Denny."

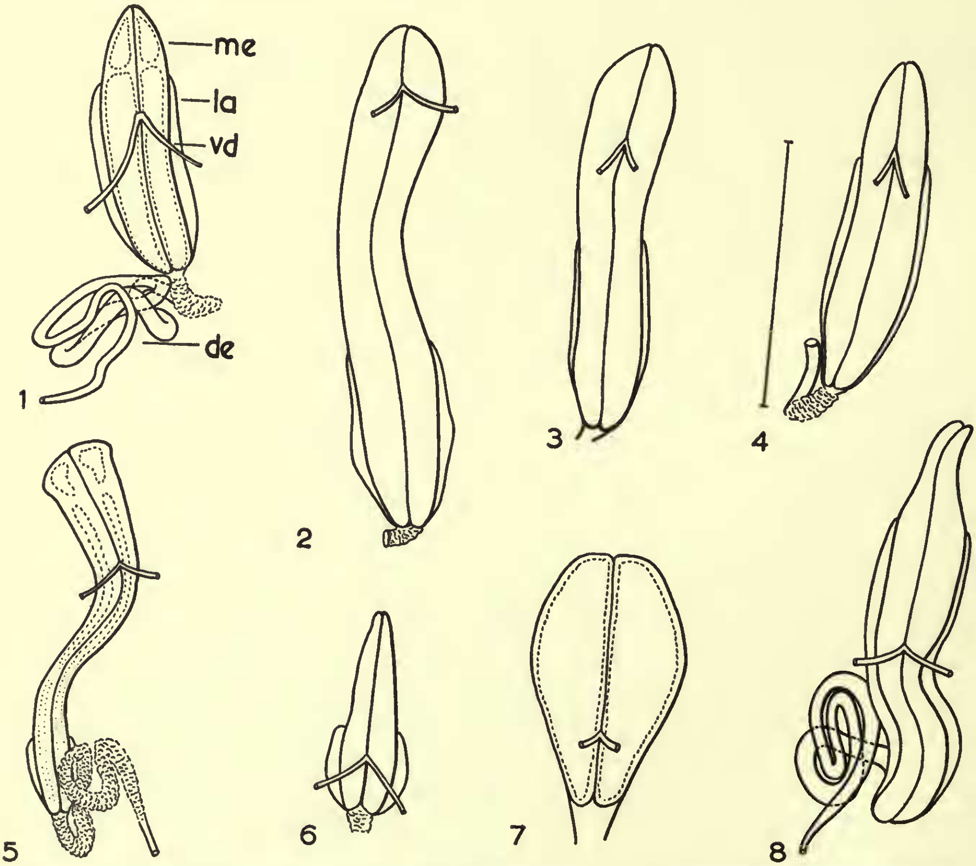
Ischnocera not exceeding 3 mm. in length ; usually without marked sexual dimorphism, but the females average larger. Usually well pigmented species, the colour pattern sometimes forming a taxonomic character. Shape of head various, anterior margin varies from pointed (*D. meinertzhageni*), flattened (*D. fulva*) or rounded (*D. leucopleura, D. discocephalus*). Marginal carina entire dorsally ; ventrally may be interrupted medially to a greater or lesser extent ; hyaline margin may be apparent as a narrow rim round the anterior margin of the head. Dorsal preantennal suture and a true dorsal anterior plate never present in adult ; the dorsal preantennal region may have thickened areas or surface sculpturing ; dorsal postantennal sutures rarely present (*D. punctifer*). Ventral carina never forms a complete semicircular band but is interrupted medially and the two carinae pass anteriorly ; at the anterior edge of the pulvinus they merge with the general sclerotization of the head and a ventral suture (the ventral preantennal suture) is carried forward to or near the anterior margin of the head. Pulvinus usually appears as a simple lobe, but in a few species (e.g. *D. guimarãesi*) each ventral carina has a sclerotized flattened part parallel to that of the other carina to which is attached a lobe of the pulvinus (see Clay, 1958). Temporal carinae absent. Mandibles similar throughout the genus ; hypopharyngeal sclerites and gular plate well developed. Male antenna usually similar to that of female, but may show marked sexual dimorphism (*D. mookerjeei*). Chaetotaxy of the head of the basic ischnoceran type (Clay, 1951) ; ocular seta and at least two of the marginal temporal setae each side elongated.

Prothorax similar throughout the group with rounded or parallel lateral margins and straight posterior margin ; one posterolateral or posterior elongated seta each side. Pterothorax may or may not show lateral indication of meso-metathoracic junction ; third episternum fully sclerotized laterally. Sternal plate narrowed anteriorly, normally with three setae each side. Dorsal pterothoracic setae usually comprise two lateral setae, one elongated and one spine-like, and four elongated setae each side of the posterior margin arranged in two pairs ; some species (*D. discocephalus*) may have a greater and more irregular number.

Abdomen with nine apparent segments in the male and eight in the female ; these are interpreted as follows : the first apparent segment, probably I and II fused, is referred to as II, the second to the seventh (the spiracle bearing segments) as III–VIII. In the male the eighth segment represents IX–X fused, the ninth is XI ; in the female the last apparent segment is IX–XI fused. Segment II is always shorter than III. The tergal plates of II–X in the male and II–XI in the female are in the form of single plates across each segment ; tergites II–III may show partial division into two sclerites. The tergite of fused IX–X in the male is usually arched and narrowed medially to a greater or lesser extent and tergal plate XI when present is a single or double sclerite immediately anterior to the anal and genital openings. Kéler (1939) has been followed in considering the dorsal plates as representing the fused tergal and pleural plates. At the lateral edge of these plates of some or all of segments II–VIII there is, in most species of *Degeeriella,* a characteristic internal thickening. This thickening, here called the pleural thickening, usually consists of an internal sclerotized buttress along the edge of each segment which is continued inwards a short way along the inner anterior margin of the dorsal plate ; there is usually a characteristic anterior part passing into the segment above, known as the re-entrant head (Waterston, 1928). Sternal plates II–VI in the form of median sclerites in both sexes ; in the male the terminal sternites form a single fused genital plate. Anal and genital openings of male on dorsal surface of the abdomen with the $3 + 3$ anal setae as described above under the definition of the *Degeeriella*-complex. The genital region of the female comprises the genital plate (i.e. sternal plate VII) usually not differing greatly from the anterior plates, but sometimes (*D. rufa*) with a median posterior prolongation. It is not possible to be certain to which segments the remaining sclerites of the genital region belong. Below the genital plate is an uncoloured area of the integument with a sclerite each side, perhaps those of VIII. The integument passes to the vulva and turns in to form the ventral wall of the genital chamber. On this wall are two sclerites, sometimes fused to a greater or lesser extent in the mid-line ; these are perhaps the median sclerites of VIII and are here called the inner genital sclerites (Text-fig. 96, *ig.*). On the dorsal wall of the genital chamber there is a sclerite each side which projects beyond the vulva ; this is perhaps the sclerite of X or IX and X fused and is here called the subvulval sclerite (Text-fig. 97, *sv*). The opening of the spermathecal tube (*os.*) lies between the subvulval sclerites in the dorsal wall of the genital chamber. The spermatheca is a simple thin-walled sac and the calyx is lightly sclerotized.

The external male genitalia (see Clay, 1956) comprise a flattened basal apodeme ; short curved parameres, the outer and inner edges of which are continuous with the basal apodeme without a point of articulation ; an endomeral plate, rather thick dorsoventrally, with diverging dorsal arms (Text-fig. 59, *da.*) which may or may not join the basal apodeme each side and two ventral arms (Text-fig. 52, *va.*) with setae. Centrally there is a sclerotized tube-like penis which usually has at its base an irregular area of sclerotization (shown in the figures by an interrupted line) joined to the basal apodeme by a narrow sclerite (the penial sclerite, *ps.*) ; at this junction there is usually a curved arm each side (the penial arm, *pa.*) bearing a seta (the penial seta, *pst.*). The dorsal and ventral endomeral arms are joined by an area passing ventro-dorsally (and not always visible) to a line of thickening each side of the ventral surface of the plate (Text-fig. 50, *a.*).

Internal male genitalia have been examined from 40 specimens of *Degeeriella* from only 19 species of hosts belonging to the Falconiformes, but even these show considerable variation. In *D. fulva* from *Buteo vulpinus* and *Buteo buteo* these structures conform in general characters to those of *Columbicola columbae* (Linn.) as described by Schmutz (1955). The vesicular apparatus comprises four separate lobes united into a single organ; as in all members of the *Degeeriella*-complex examined the two lateral lobes (Text-fig. 1, *la.*) are shorter than the median lobes (*me*); in some species of *Syrrhaptoecus* however, the lateral lobes are considerably longer than the median ones. Within each median lobe two chambers can be distinguished, the upper containing spermatozoa and the lower what is presumed to be a secretion. Each vas deferens (*vd.*) enters separately into each of the median lobes. The vesicular apparatus is continued into the ductus ejaculatorius (*de.*) which is strongly muscular near its base. The testes and vasa deferentia are similar throughout the complex, and do not differ significantly within any of the Philopteridae examined. Variation of the vesicular apparatus and the ductus ejaculatorius and the point of entry of the vasa deferentia, within the species of *Degeeriella* examined are shown in Text-figs. 1–8.

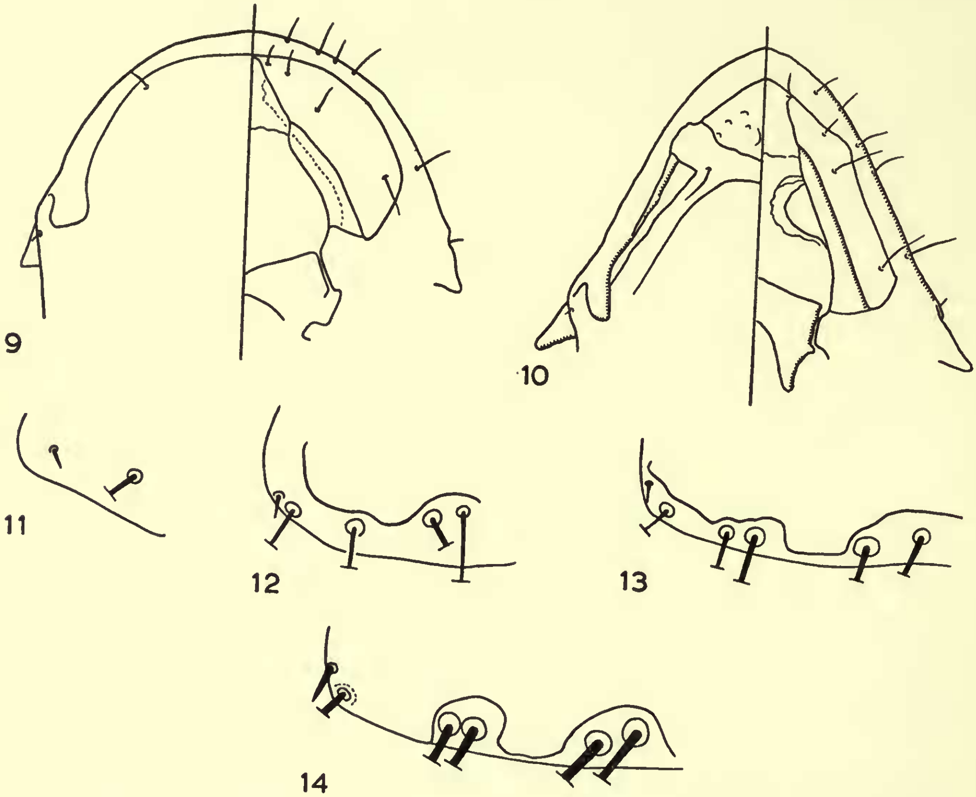


FIGS. 1–8.—Internal male genitalia of *Degeeriella*. 1. *D. fulva* from *Buteo vulpinus*. 2. *D. beaufacies*. 3. *D. fusca* from *Circus aeruginosus*. 4. *D. elani* from *Elanus caeruleus vociferus*. 5. *D. rufa* from *Falco t. rupicolus*. 6. *D. r. regalis* from *Milvus migrans*. 7. *D. mookerjeei* from *Pernis ptilorhyncus gurneyi*. 8. *D. punctifer*. *me.*—median lobe of vesicular apparatus; *la.*—lateral lobe of vesicular apparatus; *vd.*—vas deferens; *de.*—ductus ejaculatorius. Line = 0·5 mm.

The length of the median lobes and the relative size of the lateral lobes may vary considerably in different species; no lateral lobes could be seen in *D. mookerjeei*. In some cases the material was not in sufficiently good condition to distinguish the internal chambers of the median lobes, but there seems no doubt that in both *D. regalis* and *D. mookerjeei* there is only a single chamber, as spermatozoa could be seen filling the whole of the median lobes as figured for "*Lipeurus variabilis*" (? = *Cuclotogaster heterographus*, see footnote on p. 124) by Schmutz (1955 : 303). However, material suitable for sectioning is required before an accurate account can be given of the internal chambers of the median lobes. The ductus ejaculatorius is long and coiled in all species, and in all except *D. rufa* only a short basal portion is strongly muscular, in this latter species this muscular part is carried nearly to the end.

The chaetotaxy of the abdomen has the following features common to all species; the anterior tergal setae of segment II (probably those of the suppressed segment I) are two in number and elongated; postspiracular setae are present on segments III–VII with sensillae on III–V; VIII has the usual lateral seta in a sunken alveolus. All the above setae are omitted from the specific descriptions. Terga II–VIII and sterna II–VI each with a single line of setae; pleural setae present on some or all of segments III–X. Vulva with some spine-like setae and with a varying number of sensilli; posterior to the vulva there are, apart from the three anal setae, a single spine-like seta and one to three elongated setae (the pleural setae of X) each side.

Nymphs. The three nymphal instars are easily separable by the chaetotaxy of the posterodorsal margin of the pterothorax (see Clay, 1955), as shown in Text-figs. 11–14; the third instar has the setae arranged as in the adult but at least two of the setae are thinner. The head does not take on the full adult characters until after the final moult. Boetticher & Eichler (1954) have shown the differences between the shape of the preantennal region of the head in nymphs and adults in *Degeeriella* and based some of their phylogenetic deductions on these findings. The present study of *Degeeriella* nymphs from 24 species of hawks shows that the curvature of the anterior margin of the head may be approximately the same in nymph and adult as in *D. punctifer* and *D. discocephalus*; may be more rounded in the nymph as in *D. fulva* (Text-figs. 15–17) or more pointed as in *D. rufa* (Text-figs. 18–20). In *D. rufa* the anterior margin of the first instar (Text-fig. 18) resembles that of *D. fulva* to a greater extent than do those of the second or third instars (Text-figs. 19–20). The ventral carinae are sometimes better defined in the nymph than in the adult and in those of *D. rufa* (Text-fig. 10) there is a definite inner projection to which is attached a lobe of the pulvinus as in the nymphs and adults of *D. guimarãesi*; thus *D. rufa* resembles this latter species to a greater extent in the nymph than in the adult (see Clay, 1958). The second and third instars of *D. rufa* have a semicircular anterior dorsal thickening and a preantennal dorsal suture with a partial lateral break in the marginal carina each side (Text-fig. 10); these characters are not visible in the adults. In some species e.g. *D. nisus frater* both nymphs and adults have a similar dorsal anterior thickening. There may be considerable differences between the nymphs of two species: thus, although *D. rufa* and *D. fulva* are superficially rather similar the nymphs of each are markedly different (Text-figs. 9, 10). These differences are also reflected in the adults in the characters of the male genitalia, female genital region and chaetotaxy of the abdomen. *D. discocephalus* and *D. fulva* superficially distinct have rather similar nymphs. The greater similarity of the head of *rufa* in the nymphs than in the adult to that of the adults and nymphs of



FIGS. 9–14. 9–10.—Heads of third instar nymphs. 9. *D. fulva* from *Buteo jamaicensis*. 10. *D. rufa* from *Falco tinnunculus*. 11–14.—Posterior margin of pterothorax of *D. fulva* from *Buteo buteo*. 11. First instar. 12. Second instar. 13. Third instar. 14. Adult male.

D. guimarãesi is also reflected in the adults of *rufa* which have other characters in common with *guimarãesi* not found elsewhere amongst the *Degeeriella*. Populations within a species may also differ from each other to a greater extent in the nymphal than in the adult stage: the third instars of *D. rufa*, for instance, from *Falco rusticolus candicans* and *F. r. islandus* (Text-figs. 21, 22) are more different than are the adults, which in some specimens are hardly separable (figs. 143, 147). This suggests that the superficial similarity of the majority of the species of *Degeeriella* on the Falconiformes is a secondary adaptation to the environment found on this group of birds and that the characters of the nymphs may be useful in the elucidation of relationships within the genus. Some of the difficulties of understanding these relationships are mentioned below under Host Relationships.

Apart from the species of the *Degeeriella*-complex found on the Falconiformes there are two other groups which have been given generic status, but fall within the definition of *Degeeriella* as given above, these are *Capraiella* and part of *Picicola.*

Capraiella Conci, 1941. This genus was erected for *Nirmus subcuspidatus* Burmeister from *Coracias garrulus* mainly on the character of the pointed head. As will be seen below some *Degeeriella* from the hawks also have heads pointed anteriorly. It has not been possible to find any characters on which *subcuspidata* can be separated from *Degeeriella,* in fact the male genitalia considered alone would place this species near *D. fulva.* It is doubtful, therefore, whether *Capraiella* can be kept as a separate genus but further species may be found on other members of Coraciidae which may throw more light on the relationships of this group.

Picicola Clay & Meinertzhagen, 1938, and the subgenus *Tyrannicola* Carriker, 1956. This genus contains species found on the Pici and the Passeriformes, some of which can be included in the definitions of *Degeeriella* as given below. The species may lack the preantennal suture and have the tergites entire as in *Degeeriella sens. str.*, or may have a preantennal suture and divided tergal plates as in *Cuculicola.* The genitalia may be of the type found in *D. fulva* or a modification of this. These differences cut across the host divisions ; for instance, the species from *Geocolaptes* and *Thripias* belonging to the Pici and those from *Colonia* and *Sayornis* belonging to the Passeriformes have the tergites entire ; in the two former species the male genitalia are of the *D. fulva* type. The species from *Dendrocopus* (Pici) and *Pitta* (Passeriformes) have the tergites divided ; the latter species has the genitalia of the *D. fulva* type, the former the modified form. The species found on the Pici are in general less heavily sclerotized than those found on the Passeriformes and Falconiformes. It is doubtful whether the erection of numerous subgenera is the best solution of this problem.

Within the species of the *Degeeriella*-complex found on the Falconiformes three genera have been erected : *Degeeriella* Neumann, 1906 type species *Nirmus discocephalus* Burmeister ; *Kélerinirmus* Eichler, 1940, type species *Nirmus fuscus* Denny , and *Acutifrons* Guimarães, 1942, type species *A. vierai* Guimarães. *Kélerinirmus* was described to include the species with elongate heads and abdomen and to separate them from the species with round heads and abdomens represented by *D. discocephalus*, the type species of *Degeeriella.* This division, however, appears to be a purely artificial one and places together *D. discocephalus* and *punctifer* purely on shape of head and abdomen together with certain characters directly correlated with this shape and of little phylogenetic importance (Clay, 1951). In fact, the characters of the carinae and sutures of the head, the male genitalia and female genital region show that these two species are not closely related. It appears that the *discocephalus* group and *fulva* group of species, both found on the same host groups, are nearly related to each other and perhaps derived from a common ancestor on these host groups. These two species groups are for instance, more closely related to each other than either is to *rufa* in spite of the superficial similarity of *rufa* and *fulva*. Thus, it is not possible to recognize *Kélerinirmus* as a generic division of *Degeeriella*. Carriker (1956 : 114)[1] suggests the possibility that *Acutifrons* should be included in the *discocephalus* group of *Degeeriella*, but here again the similarity is purely superficial and it is unlikely that the *Acutifrons* group of species are particularly nearly related to *discocephalus*. It is possible that *Acutifrons* is not a monophyletic group, the characters distinguishing the species; the anterior dorsal suture, the temporal carinae and the enlarged head and abdomen having been developed more than once in different but related stocks. Until more is known about the distribution of these species *Acutifrons* should probably be maintained as a distinct genus.

Nirmus splendidus Kellogg, 1899. While agreeing with Carriker (1956 : 126) that the identity of this species must await the examination of the types, the description and figure are those of a *Cuculicola* not *Acutifrons*. No known species belonging to the *Degeeriella*-complex from hawks have the abdominal tergites divided medially, a character which is found throughout *Cuculicola*, further, the figure, except for the lateral margins of the temples represents the species found on *Geococcyx californiensis*. Since writing this, Carriker (1957) has been seen in which a figure is given of the male genitalia of a paratype of *Nirmus splendidus*, this seems to represent those of the species from *Geococcyx californiensis* in a somewhat compressed condition, as usually seen within the specimen. There seems little doubt that this is the true host of *Nirmus splendidus* Kellogg as figured originally by Kellogg (1899) and recently by Carriker (1957), and that the species should be included in *Cuculicola*.

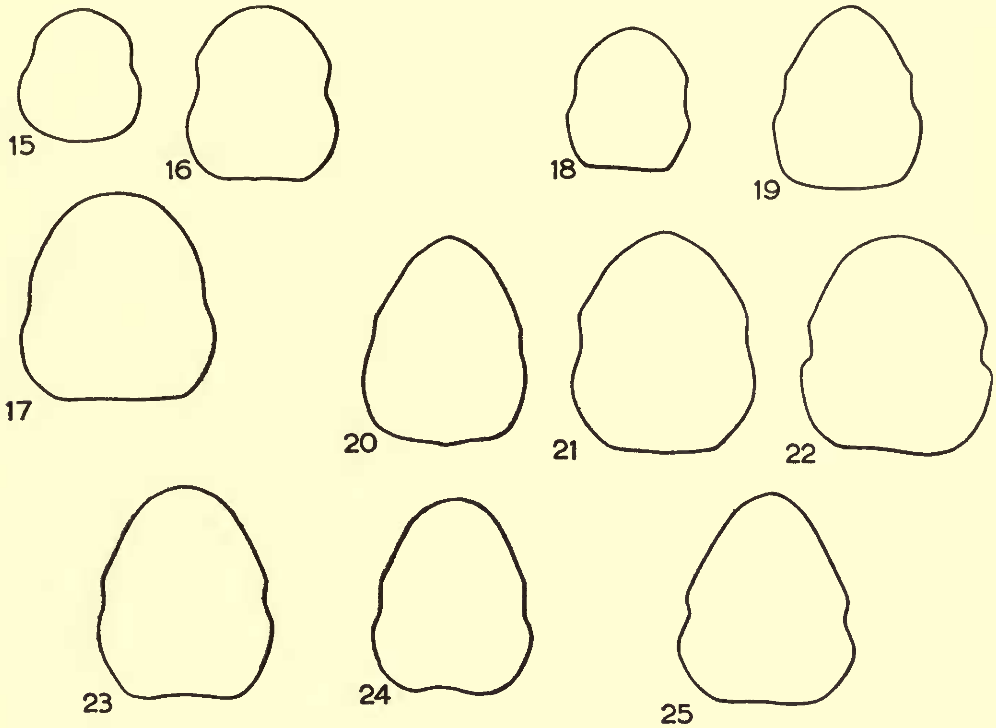
The species, subspecies and local population. In *Degeeriella* there is the difficulty, as always in the case of a widely-distributed homogenous group, of deciding whether any given form should be considered as a species or subspecies or whether some merit taxonomic rank at all. As Mayr (1951 : 93) has said, the subspecies is primarily a taxonomic concept which cannot be delimited from the local population on one hand and the species on the other. In the Mallophaga the application of the subspecific concept has been most haphazard and practically no attention has been paid to the amount of variability within populations from the same host form, and it seems that the time has come to consider this problem as a whole and to try to get some conformity within the suborder.

In the distribution of the Mallophaga it is usual for an order or suborder of birds to be parasitized throughout by the same genus (or genera) of Mallophaga. The populations[2] of this genus on the different species of birds may be apparently indistinguishable, only statistically distinguishable, or may comprise individuals which are slightly but constantly different, or which are markedly different. The present

[1] I should like to draw attention to a misquotation in this paper; on p. 114 it is stated that I use the shape of the abdomen as the principle generic character of *Oxylipeurus*; I have never considered shape of either abdomen or head as of any phylogenetic importance and as the whole of the passage to which Mr. Carriker refers was an attempt to demonstrate the dangers of using shape as a generic character in the Mallophaga it is apparent that Mr. Carriker has misunderstood what I was attempting to say, as is also shown by his remarks on p. 115, paragraph three.

[2] The word population is here used for all the individuals of a taxa of Mallophaga found on one host form which can potentially interbreed because their hosts are potentially capable of interbreeding. Thus, all the *Degeeriella* from *Buteo b. buteo* throughout its range would be considered as comprising one population.

distribution and relationships of the mallophagan genera suggest that these allopatric populations have, in general, been separated from each other by the splitting and species formation of the host stock and are thus analogous to populations of free-living animals on a group of continental islands which have been isolated by the disappearance of land connections (Clay, 1949). As in the case of such populations of free-living animals each of the mallophagan populations is an isolated unit without zones of contact with any other populations. Thus, as with all isolated allopatric



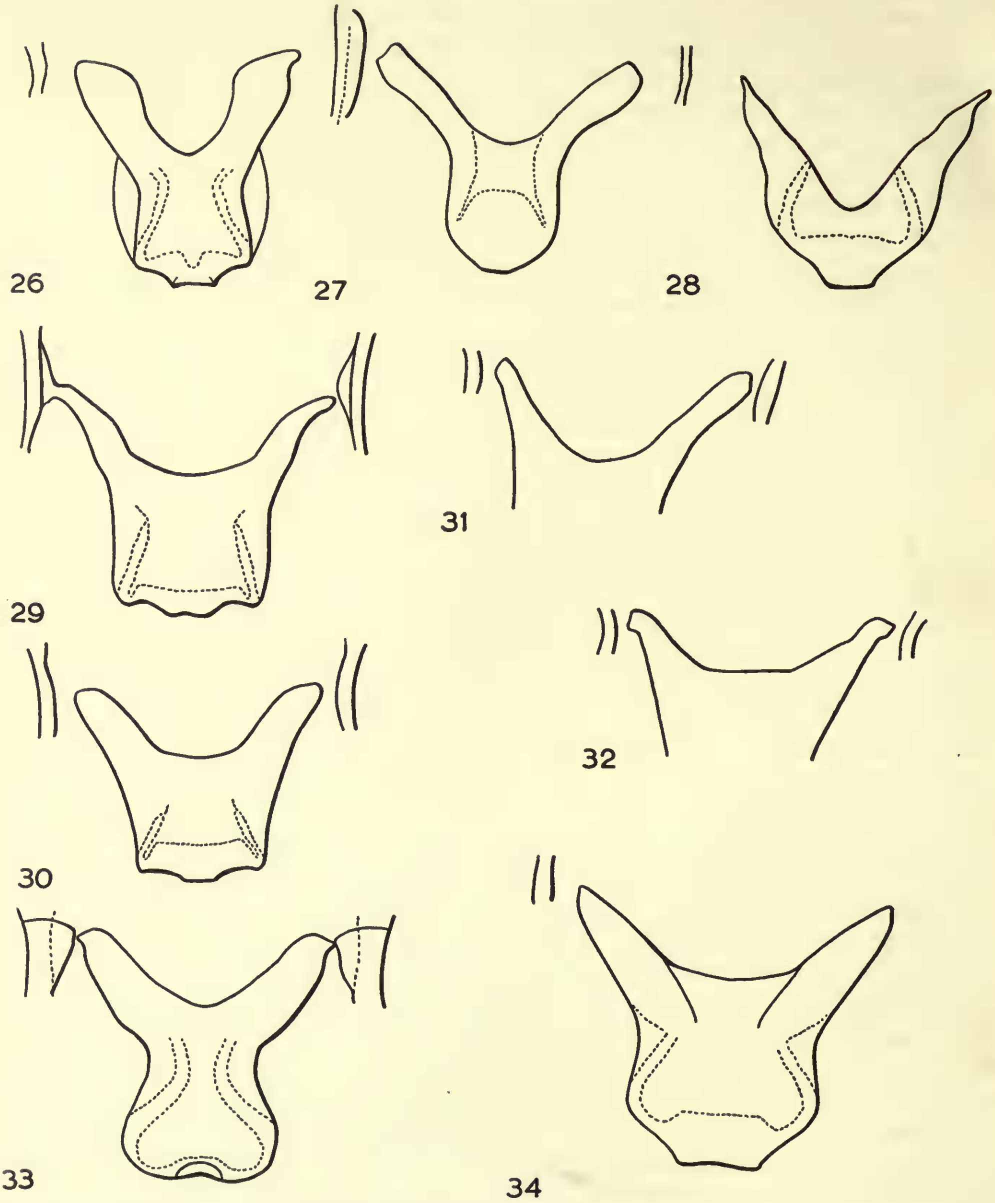
FIGS. 15–25.—Heads of nymphs. 15–17.—*D. fulva* from *Buteo buteo*. 15. First instar. 16. Second instar. 17. Third instar. 18–20.—*D. rufa* from *Falco tinnunculus*. 18. First instar. 19. Second instar. 20. Third instar. 21. Third instar *D. rufa* from *Falco rusticolus islandus*. 22. Third instar *D. rufa* from *Falco rusticolus candicans*. 23. Third instar *D. beaufacies*. 24. Third instar *D. n. nisus* frim *Accipiter nisus*. 25. Third instar *D. n. frater* from *Accipiter badius*, Thailand.

populations where there is no evidence available on the degree of reproductive isolation, there are no criteria for separating the polytypic species from the superspecies except morphological ones. As these populations are obviously allopatric replacements of each other on the different host group it might be possible in many cases to consider them as belonging to one polytypic species. But this is to ignore the morphological evidence and obscures the fact that while some show marked morphological differences others are hardly separable taxonomically. Further, some distinct populations may each have a number of related morphologically similar populations, making it more convenient to call each of these population groups, a species divided into a number of subspecies.

It seems probable that there have been two tendencies in the evolution of the Mallophaga. One was to speciate rather rapidly, perhaps due to the original occupation of an empty ecological niche provided by the feathered bodies of birds, a changing environment due to the evolution of the birds themselves, together with the increasing isolation of the populations of the Mallophaga. The second tendency was a conservatism due to the later similarity of the environments afforded by birds belonging to one group, and to the close adaptation to a host which results from the parasitic habit and perhaps limits subsequent morphological change. The first tendency was probably responsible for the formation, in the Ischnocera, of the large number of genera and distinctive species groups, while the second has led to the similarity of the forms comprising these groups. The uniform environment and the necessity of being able to move easily through the feathers has probably been responsible for the relatively smooth uniform surface of the Mallophaga without the development of feathered setae, scales and other modifications of the exoskeleton which provide useful taxonomic characters in many groups of insects. It is rather frequent in the genera of the Ischnocera to find a series of populations superficially similar and differing mainly in the characters of the male genitalia, the uniformity of the environment having led to superficial similarity and the isolation of the populations being shown in differences in such non-adaptive characters as the male genitalia. It must be expected in the Mallophaga that the character differences between related groups will be small, and these must of course be judged for each group of related species ; similar character differences cannot of course be used in separating analogous taxa in the Ischnocera and Amblycera, for instance.

The degree and time of isolation cannot be used to determine the specific or subspecific status of a population : the populations of *Degeeriella* (*D. regalis regalis*) on *Milvus* and on *Buteo galapagoensis* are separated by host and geographical distribution, and although there cannot have been any gene flow between these populations over great periods of time, and although the gene pools must now be distinct, there is no clear cut morphological difference between these populations. If distribution is taken into account there is a further difficulty that the exact relationship between the hosts is not always known, so that on the analogy of the free living allopatric populations the exact position of the locality of any one population in relation to another is uncertain and deductions of which are the most nearly related populations cannot always be made. Thus, although some groups may show gradients in such characters as the size and shape of head and number of abdominal setae these cannot be equated with clinal variation in free-living populations, as the populations are isolated and they have a host (not geographical) distribution, the most similar forms not necessarily being most nearly related. For instance, in *Degeeriella* there are examples of Harrison's law that in related populations those parasitizing the larger hosts tend to comprise larger individuals ; correlated with this increase in size there is a tendency towards larger heads, broader anteriorly, and sometimes to a greater number of abdominal setae. This tendency is seen in some of the populations of *D. rufa* on *Falco*, *D. nisus* on *Accipiter* and *D. fulva* on *Buteo*. Thus, sometimes the similarity of characters is partly due to ecological factors and not relationship (although in some cases of course the former may be dependent on the latter). Some of the subspecies in the Mallophaga differ from each other in only one character or in two or three correlated characters perhaps associated with size differences which are themselves dependent on host size. Thus, there may be populations, not very closely related, which are indistinguishable from each other and must be included in the same subspecies (Mayr, Linsley, Usinger, 1953 : 32); these are analogous to the polytopic subspecies of the free-living animal.

It has been suggested (Mayr *et al.*, 1953 : 104) that the morphological differences between sympatric species of the same genus might give an indication of the correct status of isolated populations, but Brown & Wilson (1956 : 49) have shown that when two species of animals overlap geographically the difference between them is accentuated in the zone of sympatry and weakened or lost entirely in parts of their range outside this zone. This might explain the differences between the species of *Degeeriella* (a genus in which sympatry is rare) on *Pernis*, which are so much greater than is usual between species found on hawks belonging to the same genus. The two species, *Pernis apivorus* and *P. ptilorhynchus* might originally have had the same species of *Degeeriella*, the populations of which split into two and diverged sufficiently to remain distinct when they later became sympatric (see Clay, 1949); if the fact that that they had become sympatric caused them to diverge to a greater extent and if *D. phlyctopygus* became extinct on *Pernis ptilorhynchus* and *D. mookerjeei* on *P. apivorus*, the differences between these two species of *Degeeriella* would be more marked than if they had not formerly been sympatric. This explanation is partly supported by the fact that these two species are separated by the characters of the male antennae, a common difference between sympatric species of the same genus (Clay, 1949). It is perhaps for this reason that differences between allopatric species are sometimes much smaller than those distinguishing sympatric species. If we accept the definition of subspecies as populations which would interbreed under natural conditions if they occurred sympatrically, then any morphological differences which might prevent interbreeding should be considered as specific characters. It seems reasonable to suppose that at least some of the character differences between closely related sympatric species are those which prevent or discourage cross-breeding. In the Ischnocera closely related sympatric species may be distinguished by the male genitalia, male antennae and in one genus (*Osculotes*) the legs of the male, and in size and proportions of the head and abdomen. The former characters would probably all prevent or discourage cross-breeding, while the last two characters might mean that the populations were partly restricted to different ecological niches on the body of the bird resulting in partial isolation from each other. An example of this in the Anoplura is provided by *Pediculus humanus humanus* and *P. h. capitis*, whose occupation of different ecological niches on man has resulted in impaired fertility when they are crossed (Hopkins, 1949 : 419). Even gross differences in the form of the male genitalia in insects may not form a mechanical bar to successful copulation (Dobzhansky, 1955 : 189). Jordan (1896) in his analysis of the genitalia of *Papilio* showed that in general each of the species was distinguishable by the form of the male genitalia; he also showed that there was geographical variation



FIGS. 26–34. Endomeral plate, dorsal view. 26. *D. fulva* from *Aquila chrysaëtos.* 27. *D. carrikeri.* 28. *D. emersoni.* 29. *D. n. nisus* from *Accipiter n. nisus.* 30. *D. fusca* from *Circus aeruginosus.* 31–32.—*D. n. frater* from *Accipiter badius,* Thailand; 2 specimens from the same host individual to show variation. 33. *D. hopkinsi.* 34. *D. leucopleura.*

in the structure of the male genitalia and concluded that it was not possible to draw a distinction between specific and subspecific characters and that a peculiarity of a structure might be an individual aberration, a subspecific or a specific character. Jordan did, however, believe that divergence in the organs of copulation was a means of preventing intercrossing. Within the Mallophaga the genitalia may be uniform, with only minor or no apparent differences throughout genera, or large species-groups, examples of this are found mainly in the Amblycera (e.g. *Colpocephalum* and *Actornithophilus*), and in some Ischnocera (e.g. *Anaticola*) ; in others there may be relatively small but constant differences in the population from nearly every host species, as in some groups of *Quadraceps*, and in other genera the differences may be so great that it is difficult to homologize the sclerites forming the genitalia of the different species. It must, therefore be presumed that the differentiation of the genitalia has taken place at different rates in different groups and that similarity of genitalia cannot always be used as a criterion of conspecificity, this is especially so in some genera of *Amblycera*. In *Anaticola* again, where the genitalia are similar throughout the genus it would seem to be necessary to use the characters of the preantennal region of the head for specific divisions. It is clear therefore, that the delimination of the specific and subspecific categories in the Mallophaga must be based on criteria which differ in each genus and that a study of the whole genus is necessary before a decision on these categories is made. Moreover, it is necessary to choose completely arbitrary criteria for the decision as to whether a population should have specific or subspecific rank, and this, in spite of some of the criticisms mentioned above, must be based on the characters of the genus as a whole, the number of character differences present, the characters separating sympatric species of the same genus and to a lesser degree host distribution.

It is apparent that the male genitalia of the *Degeeriella*-complex (see above p. 124) are rather constant in character, those of *Capraiella*, for instance, being quite near the *fulva* group of species, and that small differences in these structures may therefore be of significance in distinguishing species. A population has been considered as a full species if the individuals comprising it show one of the following qualifications :

1. Male genitalia quite distinct.

2. Male genitalia differ to a lesser extent, sometimes to a rather minor degree, but there are also a number of other character differences, such as the presence or absence of the pleural setae on certain of the abdominal segments, 4 or more setae on each of the sterna III-VI, together with other morphological characters such as the form of the pleural thickening, marginal carina and ventral suture of the head, and marked differences in the shape of the nymphal heads.

3. Male genitalia apparently indistinguishable but the individuals differ in many of the other characters listed above.

Populations are treated as subspecies when the male genitalia are apparently identical or only differ to a minor degree (e.g. number of setae as in *D. rufa caruthi*), which differ in the shape and proportions of the head and in a minor way in the breadth of the temporal marginal carinae and pleural thickenings or the shape of various sclerites.

The second, and more controversial problem is that of deciding whether certain populations should be recognized taxonomically at all. Various procedures have been adopted within the classification of the Mallophaga, one is to describe as new every population occurring on a different host species, in the hope, it is presumed, that 50% or more may prove to be valid and leaving some other worker to find out. Another method is to take single specimens and to describe them as new species or subspecies on some minor character which is likely to be variable within the population or even an artefact due to method of preservation and of no taxonomic significance. These two examples of bad taxonomic procedure, unfortunately still rather frequent in the systematics of the Mallophaga, need not be further considered. The difficult cases are those where there are differences and where the populations must be genetically quite distinct, but it is considered unsatisfactory to recognize them taxonomically. In *Degeeriella* it is possible to distinguish three categories, apart from those where insufficient material is available, the taxonomic recognition of which it is considered would not assist in the classification of the group :

1. Certain populations are only separable from each other statistically ; here no useful purpose would be served in naming these microsubspecies, where many individuals would not be identifiable.

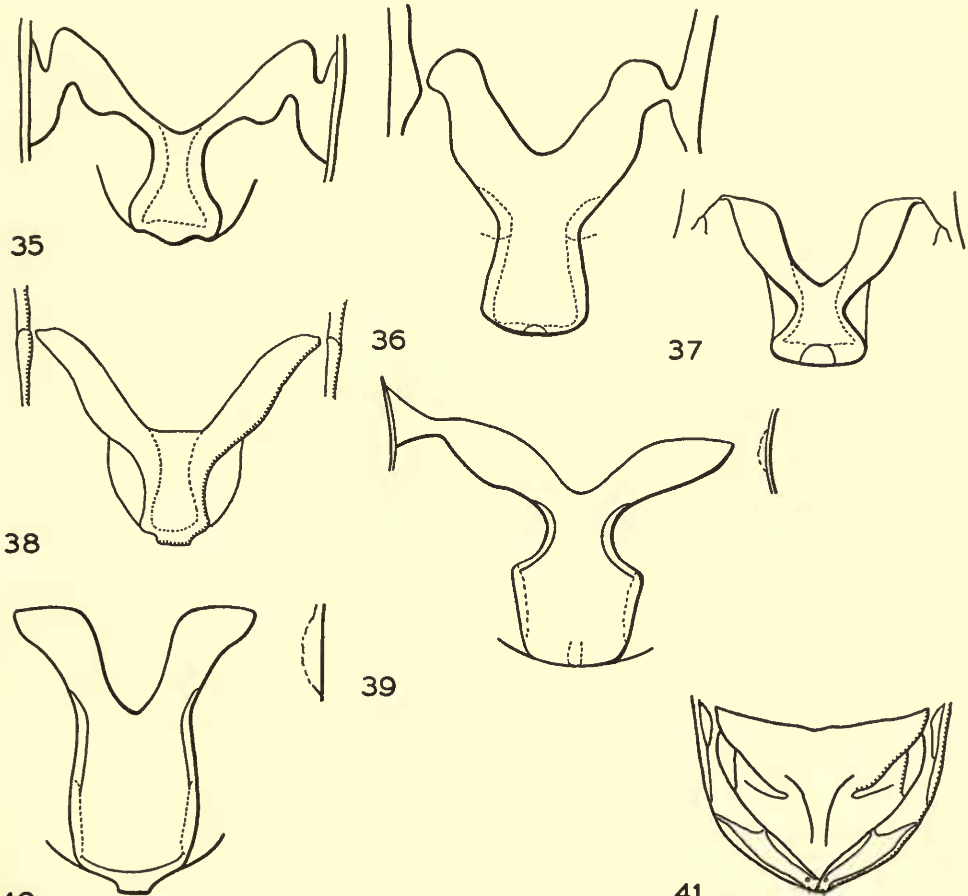
2. Certain populations may appear to differ, but when large series are examined too much variation is found to support the divisions, an example of this are the populations from *Aquila* and the various species of *Buteo* (see p. 146).

3. The populations from two hosts may be distinctly separable on such characters as size and shape of head, but if between these two there is a series of populations from related hosts showing a character gradient in these characters it is not considered that any of the populations should be recognized. The populations of *D. rufa* from *Falco* provide a particularly difficult problem (see further p. 183) as they differ from each other in the outline of the anterior margin of the head, showing all degrees from marked differences to very slight ones, the latter being complicated by individual variation. If any subspecies are recognized then the classification of the populations showing minor differences becomes almost impossible ; this may be a case where subspecies should not be recognized.

This policy of not overwhelming the classification by naming every statistically or barely separable population is not to discourage the study of populations, their variation and host distribution ; there is much interesting information on these subjects to be gathered from detailed statistical analysis, all that is here recommended is that these populations should not be given names. In this present paper an attempt has been made to sort out the populations deserving taxonomic rank and not to study detailed variation.

Variation and artefacts. The populations of *Degeeriella* from the various hawks are frequently very similar to each other and forms are separated on rather slight character differences, for this reason it is necessary to consider the amount of variation within populations from one host form. Further, it is necessary to work with specimens which have been treated in various ways so that they can be examined under high-power microscopes and this may cause various artefacts dependent on the methods used. Individuals in populations of Mallophaga, unlike some other groups of insects, tend to show little variation in size and external characters, due no doubt to the similarity of the environment in all stages of development and to the unlimited and easily accessible food supply. The reliability of the morphological characters which have been used in the taxonomy of the group are discussed below.

1. *Size.* As already mentioned populations of Mallophaga tend to be rather constant in size. A number of experiments were carried out to see which was the most reliable measurement in *Degeeriella*. A male and female of each of *D. fuva*, *D. r. regalis* and *D. rufa* were measured at each stage of the following treatments :



FIGS. 35–41. Endomeral plate, dorsal view. 35. *D. d. discocephalus.* 36. *D. elani.* 37. *D. tendeiroi.* 38. *D. rufa* from *Falco tinnunculus.* 39. *D. r. regalis* from *Milvus milvus.* 40. *D. r. deignani.* 41. *D. punctifer.*

(*a*) In 80% alcohol after two to three years storage ; (*b*) in a saturated solution of phenol in 70% alcohol, warmed to clear ; (*c*) after 22 hours in cold 10% caustic potash, body contents removed, cleared in clove oil and mounted in canada balsam ; (*d*) after immersion for 15 minutes in 10% caustic potash in a boiling water bath, mounted in canada balsam and the cover glass pressed well down. It was found the breadth of the temples remained either constant under the different treatments or changed no more than 0·004 mm., while other measurements especially total length, breadth of pterothorax and length and breadth of abdomen were rather variable due to contraction or expansion between the different regions of the body or changes in shape due to pressure by the cover slip. This means that in *Degeeriella* the breadth of the head is a measurement that can be taken quickly and accurately in any media, does not alter with the age of the adult, the abdomen for example in teneral females is usually smaller (Clay, 1956) and it is possible to compare the measurements of other workers as there is no ambiguity about the exact position of where the measurement is taken. The whole of the collected populations from one bird can be measured in phenol solution without the labour of mounting them in canada balsam and ensures that not only the larger specimens, which consciously or unconsciously are likely to be picked out for permanent mounts, are measured. This measurement, therefore, is useful in comparing populations from various hosts which differ only in absolute size ; the size of the temple breadth being roughly proportional to the total size. It cannot of course be used in comparisons of populations which differ in the shape of the postantennal region of the head. It should be noted that this is a different problem from the consideration of which measurements show the least variation in a population from one host where all individuals have been treated in the same way. Tjønneland (1955) compiled the variation coefficients for various measurements of 40 males and 40 females of *Degeeriella d. aquilarum* Eichler taken from the same host individual and subjected to the same treatment ; it was found that the measurement of the head showed the least variation within the populations. It has been found in numbers of specimens belonging to one species that those from the different hosts may differ in average measurements of head breadth, but that the ranges overlap ; it is important therefore to give the range and number of specimens measured. For reasons discussed elsewhere (p. 138) time has not been spent on statistical analysis of the measurements of the different populations of *Degeeriella* mentioned in this paper. It is doubtful whether subspecies should be recognized on size differences alone and certainly not when only two or three specimens are available.

2. *Pigment and sclerotization.* As it is frequently necessary to work with material which has been kept long in alcohol or over treated with caustic potash it is difficult to use the characters in the comparison of all species. However, the amount and arrangements of pigment may be a taxonomic character (see *D. fusca*). The sclerotized plates may vary in outline as some of these, especially the thoracic sternal plates and the male and female genital plates, may have part of the plate more lightly sclerotized and in some specimens, either naturally or due to treatment, the lighter part is not apparent, thus altering the outline.

3. *Head.* The shape and size of the head is a useful character and as shown above the breadth is not affected by the various methods of preparation. However, in some populations there appears to be a certain amount of variation in the curvature of the anterior margin (see under *D. fulva*). The thickness of the marginal carina and the presence or absence of an inner median indentation are usually reliable characters, but there may be intrapopulation variation in these characters, sometimes due to methods of preparation ; teneral specimens especially may be misleading in

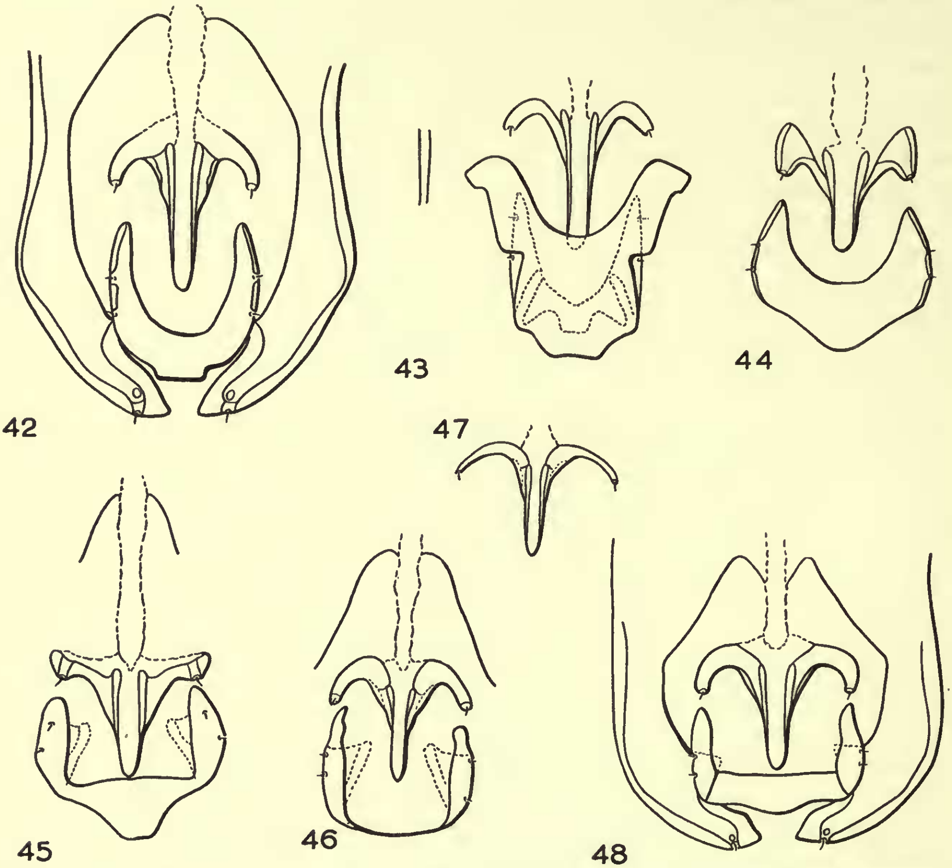
these characters (see below under *D. pseudophaea*). Thus, specimens of the *fulva*-group from the same host form may have the typical flattened anterior margin, with broad marginal carina and well marked inner marginal indentation, whereas other specimens may have rather rounded anterior margins, rather narrow marginal carina and the inner marginal indentation not apparent. Specimens which have been left too long in caustic potash may have the marginal carina appearing narrower, the head often more rounded anteriorly and the anterior end of the ventral suture not distinguishable; the extent of the hyaline margin may also vary in mounted specimens according to the position and pressure exerted. The proportions of the head, that is ratio of length of preantennal region to postantennal region and ratio of breadth to length of these regions may be misleading as these show variation within populations. Reduction of these proportions to mathematical terms is unsatisfactory owing to the difficulty of finding exact points of measurement and a more accurate method is that described in Clay & Hopkins (1954 : 230) in which an outline of a head is drawn with a camera lucida and comparisons of other heads made by projecting them on to this outline ; by adjusting the magnification it is possible to get a fixed measurement such as the breadth of the temples and thus compare the proportions of the head (see also p. 184). If this is done with a large number of specimens from one host it will be seen that proportions are often variable and cannot be used for subspecific divisions. Both the marginal and temporal marginal carinae may have indentations, the number, shape and position of which show some individual variation. However, the thickness and outline of these carinae, with the reservations discussed above, may be of taxonomic importance. The conus tends to be variable in shape and length mainly due to the position in mounting and except where the differences are strongly marked (e.g. *D. punctifer*), this structure has not been used as a taxonomic character. The position of the second ventral submarginal seta (Clay, 1951) shows individual variation being found either above or below the level of the inner margin of the marginal carina.

4. *Thorax.* The number of sternal setae and the shape of the sternal plate show individual variation (Text-figs. 112–118). and is of no taxonomic value amongst nearly related species. There are usually eight elongated posterodorsal setae on the pterothorax arranged in two groups of two each side, but there may be individual variation in the number and position.

5. *Abdomen.* In general the presence or absence of a partial division of tergal plate II–III is constant for a given taxa, but there are cases where this character especially in II shows individual variation. The width and the dorsal and ventral outline of the pleural thickening is often a useful character, but in mounted specimens is liable to distortion ; this distortion is particularly marked in the shape and details of the re-entrant head ; teneral specimens do not always show the normal characters of the adult pleural thickening. In the female the subvulval sclerites may show slight individual variation.

6. *Male genitalia.* The basal apodeme may show slight variation in outline either due to individual variation or to distortion in preparation. The shape of the tips of the parameres must again be used with caution as the appearance of these is dependent on position of mounting. The sclerotization round the penial sclerite and penial

arms is irregular and rather variable in outline. The fusion or not of the dorsal endomeral arms with the basal apodeme may be a specific character or it may show individual variation and differ on the two sides of the same individual. There is also frequently considerable variation in the shape and length of the distal ends of



FIGS. 42–48. Male genitalia, ventral view of distal area. 42. *D. fulva* from *Aquila chrysaëtos*. 43. *D. beaufacies*. 44. *D. carrikeri*. 45. *D. emersoni*. 46. *D. n. nisus* from *Accipiter nisus*. 47. *D. n. frater* from *Accipiter badius*, Kenya. 48. *D. fusca* from *Circus aeruginosus*.

the ventral endomeral arms and the position of the setae, the two sides in one individual often being asymmetrical in these characters. It is not always possible to see the relationship of the dorsal and ventral parts of the mesosome to each other unless the genitalia are dissected and mounted separately on the slide.

7. *Abdominal chaetotaxy*. This frequently forms a useful taxonomic character, but it is important to consider the amount of individual variation. The presence or absence of pleural setae on some of the anterior segments and on X in the male can be used to separate species or species groups, but occasionally an individual will

be found with one seta present on one side of a segment when its absence is characteristic of the species. Another character which can be used to separate species groups is whether the sterna of III–VI normally have 4 or more setae ; however, the species characterized by the presence of 4 setae may have the occasional specimen with one or two segments with 3 or 5 setae. The number of tergal setae may also be taxonomically important but here again there is individual variation and a more useful character is the range in the total number of setae found on segments III–VII. The dorsal setae on segment X of the male may vary from 1–3 each side, but in some populations one each side seems to be the rule with occasional exceptions.

Characters of taxonomic importance. The following characters have been found to be of taxonomic importance in *Degeeriella* and should be given together with their variation in all descriptions of new taxa : Shape of head : form of marginal and ventral carinae, and anterior extension of ventral suture ; thickness of temporal marginal carinae ; number of elongated marginal temporal setae ; presence or absence of postantennal sutures. Form of tergal plates of segments II–III, and XI in male and IX–XI in female ; width, and dorsal and ventral outline, and development of re-entrant head of pleural thickening. Outline of female genital plate, inner genital sclerites and subvulval sclerites. Presence and absence of pleural setae on segments II–VI and of X in male and numbers of sternal setae. The male genitalia should be figured to show the length of the penis and the form of the penial arms, and a dorsal and ventral view of the endomeral plate.

SYSTEMATIC SURVEY OF THE SPECIES OF *DEGEERIELLA* PARASITIC ON THE FALCONIFORMES

For convenience in classification and to avoid frequent repetition in descriptions, the species are divided into a number of species groups. There is naturally not always a clear cut distinction between the species groups and these may not always form natural phylogenetic assemblages. The groups are based mainly on the characters of the head, abdominal chaetotaxy and the male genitalia. Characters given under the definition of the genus (p. 126) and for the species groups are not usually repeated again in the descriptions of the species.

The fulva *Species Group*

1. Head index less than 0·90.
2. Dorsal head sutures not apparent.
3. Two of the marginal temporal setae each side elongated.
4. Thoracic sternal plate and chaetotaxy as in Text-figs. 112–118 ; this plate shows individual variation in shape and in the number of associated setae.
5. Thorax and abdomen with general shape as in Pl. 1, fig. 1.
6. Tergal plates of segment XI not apparent in male.
7. Terga of segments IX–XI in female as in Text-fig. 105.
8. Pleural thickening of segments III–VI usually with well developed re-entrant heads.

9. Sternites of II–VI in the form of quadrilateral median plates.
10. Male genital plate of irregular and variable outline.
11. Female genital plate without median posterior prolongation.
12. Female inner genital sclerites never fused in mid-line.
13. Male genitalia of type shown in Pl. 8, fig. 3; penial sclerite present.
14. Setae each side of posterodorsal margin of pterothorax: 1 (lateral) spine-like seta, 1 elongated seta, 2 pairs of elongated setae (as Text-fig. 14).
15. Pleural setae absent on segments II–III and usually IV, and on segment X in male.
16. Sternocentral setae of segments III–IV normally 4.
17. Ventral chaetotaxy of male segments VII–XI as in Text-fig. 102; in some specimens one or both of the outer setae on segment VII may be absent.

Degeeriella fulva (Giebel), 1874

Type host: *Aquila chrysaëtos* (Linn.)

(Pl. 1, figs. 1–7; Pl. 8, fig. 3; Text-figs. 1, 9, 11–17, 26, 42, 70, 84, 102, 105, 109, 112–118)

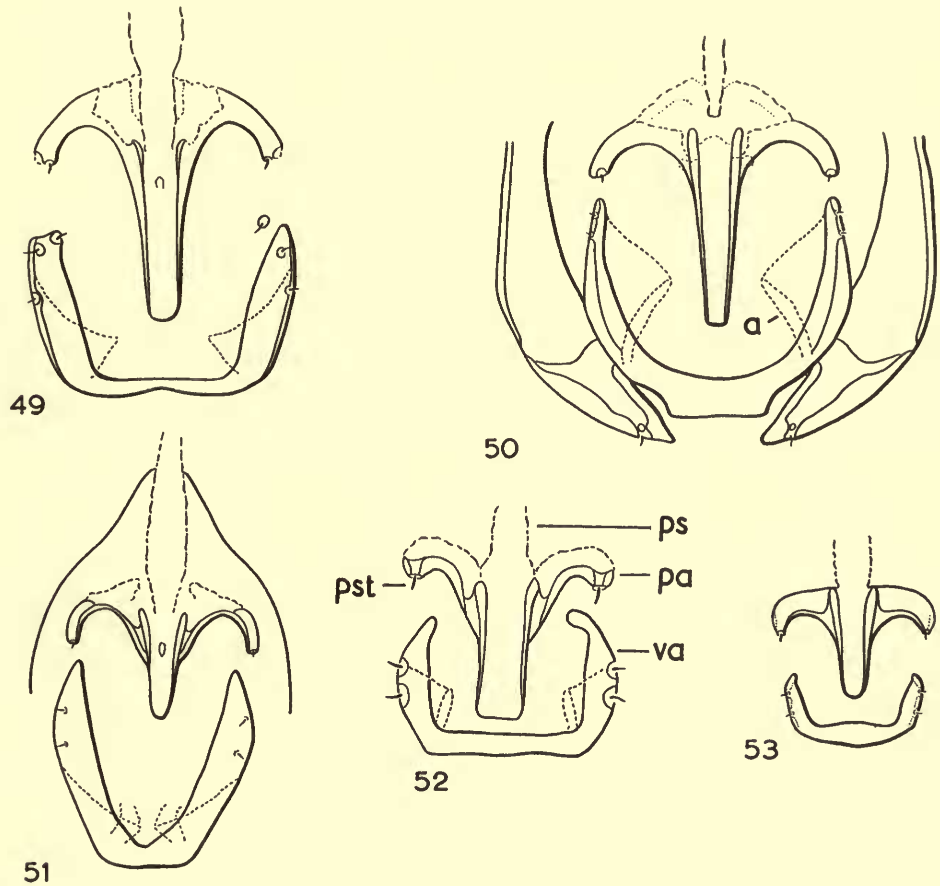
Nirmus fuscus Nitzsch, 1861, *nec Nirmus fuscus* Denny, 1842. *In* Giebel, *Z. ges. Nat Wiss.* **17**: 525. Host: *Buteo vulgaris* = *Buteo b. buteo* (Linn.).
Nirmus fulvus Giebel, 1874. *Insecta epizoa*: 124. Host: *Aquila fulva* = *A. chrysaëtos* (Linn.).
Nirmus angustus Giebel, 1874. *Insecta epizoa*: 126. Host: *Buteo lagopus* (Pontoppidan).
Nirmus flavidus Giebel, 1874. *Insecta epizoa*: 301, Host: *Buteo jaktal* = *Buteo r. rufofuscus* (J. R. Forster).
Degeeriella giebeli Hopkins, 1947. *Entomologist*, **80**: 77. Host: *Buteo b. buteo* (Linn.).
Degeeriella borealis Carriker, 1956. *Florida Ent.* **39**: 41, figs. Host: *Buteo jamaicensis borealis* (Gmelin).
Degeeriella genitalis Carriker, 1956. *Florida Ent.* **39**: 43, figs. Host: *Buteo regalis* (G. R. Gray).

The description, figure and host of *D. fusca* (Nitzsch) make it certain that this name, already preoccupied, is a synonym of *D. fulva* (see also Hopkins, 1947: 76).

The original description of *D. fulva* together with the fact that it was placed between *fuscus* and *rufus*, both figured, show that Giebel's original specimen must have been the elongated type (Pl. 1, fig. 1) of *Degeeriella* found on *Aquila* not the round-bodied type (Pl. 9, fig. 2). As this species appears to be indistinguishable from that on *Buteo* there seemed a possibility that the known specimens might have been stragglers from this latter genus. However, an examination of all the available material from *Aquila*, that is 18 ♂, 36 ♀ from nine individuals of seven species of *Aquila*, shows there is no doubt that *Aquila* was the true host of at least three of these records; the hosts of the remainder cannot now be confirmed. It can be assumed, therefore, that the species described below is a natural parasite of *Aquila*.

Degeeriella fulva is distinguishable from other species in the species group by a combination of the characters of the marginal carina, ventral suture, tergites II–III, pleural thickening, number of pleural setae and the details of the male genitalia.

MALE. Inner dorsal margin of marginal carina indented medially ; ventral suture passes to anterior margin of head (Text-fig. 109, *v.*). Tergite II only with definite median unsclerotized indentation. Pleural thickening narrow with inner edges comparatively straight. Genital plate as in Text-fig. 102. Genitalia as in Pl. 8, fig. 3 and Text-figs. 26, 42 ; there is some variation in the shape of the basal apodeme



FIGS. 49–53. Male genitalia, ventral view of distal area. 49. *D. hopkinsi*. 50. *D. leucopleura*. 51. *D. d. discocephalus*. 52. *D. elbeli*. 53. *D. tendeiroi*. *ps.*—penial sclerite ; *pa.*—penial arm ; *pst.*—penial setae ; *va.*—ventral endomeral arm.

and of the base of the endomeral plate which does not always show an inner indentation. Internal genitalia as in Text-fig. 1.

FEMALE. Terga of segments IX–XI as in Text-fig. 105 and genital region as in Text-figs. 70, 84.

CHAETOTAXY OF ABDOMEN. Tergocentral setae : II normally 6[1] range 4–7 ; III–V normally 8, range 6–8 ; VI–VIII normally 6, range 4–8. X in the male has

[1] In this and all subsequent descriptions the two anterior setae always found on II are omitted.

from 1–3 setae each side ; of 16 males from *Aquila* 11 had one (1 + 1) each side, 3 had 1 + 2 and two had 2 + 2 ; in 80 males taken at random from various species of *Buteo*, 8 had 1 + 1, 19 had 1 + 2, 44 had 2 + 2, 7 had 2 + 3 and 2 had 3 + 3. Tergal setae of segments X–XI of female as in Text-fig. 105. Pleural setae : II–IV 0 ; V, 1 on each side ; VI–VII, 2 ; VIII, 3. In the male IX has 2 each side and X, 0. In the female IX and X each have 1–3 each side. Sternocentral setae of II–VI normally 4 with the occasional segment of the occasional specimen with 3 or 5. In the male total number of marginal setae of last segment dorsal and ventral, varies from 9–14.

NYMPHS. No nymphs have been seen from any species of *Aquila* ; pterothoracic setae and heads of the three instars of specimens taken from *Buteo* are shown in Text-figs. 9, 11–13, 15–17.

VARIATION AND HOST DISTRIBUTION. The detailed comparison made by Tendeiro (1955 : 590) between specimens from *Buteo buteo* and *Aquila chrysaëtos* has been studied closely, but the conclusions reached are different ; this is probably due to the availability of specimens from a greater number of species of *Aquila* and *Buteo*. Through the kindness of Dr Tendeiro it has been possible to examine three males and six females from *Aquila chrysaëtos* ; these have been compared with 15 males and 30 females from six other species of *Aquila* and about 350 males and 400 females from 17 forms of *Buteo*. Certain characters were found to be too variable within the

Measurements in mm.

Male

	A		B			
			Length		Breadth	
	Length	Breadth	Range	Mean	Range	Mean
Head	0·53	0·43	0·50–0·58 (17)	0·55	0·38–0·45 (17)	0·43
Prothorax	—	0·30	—	—	0·25–0·30 (12)	0·27
Pterothorax	—	0·47	—	—	0·42–0·47 (12)	0·45
Abdomen	1·18	0·58	1·02–1·25 (10)	1·14	0·50–0·67 (10)	0·58
Total	2·06	—	1·83–2·20 (11)	2·02	—	—
Genitalia*	0·34	—	0·34–0·38 (4)	0·37	—	—
Head index	0·81	—	0·75–0·79 (17)	0·77	—	—

Female

	A		B			
	Length	Breadth	Length Range	Length Mean	Breadth Range	Breadth Mean
Head	0·60	0·47	0·58–0·62 (12)	0·59	0·45–0·49 (12)	0·47
Prothorax	—	0·30	—	—	0·28–0·33 (10)	0·29
Pterothorax	—	0·50	—	—	0·47–0·53 (10)	0·50
Abdomen	—	—	1·13–1·43 (9)	1·17	0·60–0·70 (10)	0·65
Total	—	—	2·03–2·35 (9)	2·23	—	—
Head index	0·78	—	0·77–0·81 (11)	0·79	—	—

A. Single specimen from *A. chrysaëtos*. B. Specimens from *Buteo lagopus*.

* Length of genitalia of male taken from anterior margin of basal apodeme to posterior margin of endomeral plate. Number of specimens measured given in brackets. Head index = breadth : length.

C

Male

	Length			Breadth	
	Range	Mean		Range	Mean
Head (10)	0·50–0·55	0·53	.	0·40–0·43 (12)	0·42
Prothorax (7)	—	—	.	0·25–0·28	0·26
Pterothorax (7)	—	—	.	0·40–0·47	0·43
Abdomen (7)	1·03–1·22	1·13	.	0·50–0·60	0·54
Total (7)	1·80–2·10	1·96	.	—	—
Genitalia (4)	0·33–0·37	—	.	—	—
C.I. (10)	0·77–0·80	0·79	.	—	—
Female					
Head (9)	0·55–0·58	0·57	.	0·44–0·46	0·45
Prothorax (9)	—	—	.	0·27–0·28	0·28
Pterothorax (8)	—	—	.	0·46–0·49	0·47
Abdomen (7)	1·27–1·38	1·32	.	0·58–0·62	0·60
Total (7)	2·15–2·30	2·22	.	—	—
C.I. (9)	0·76–0·80	0·78	.	—	—

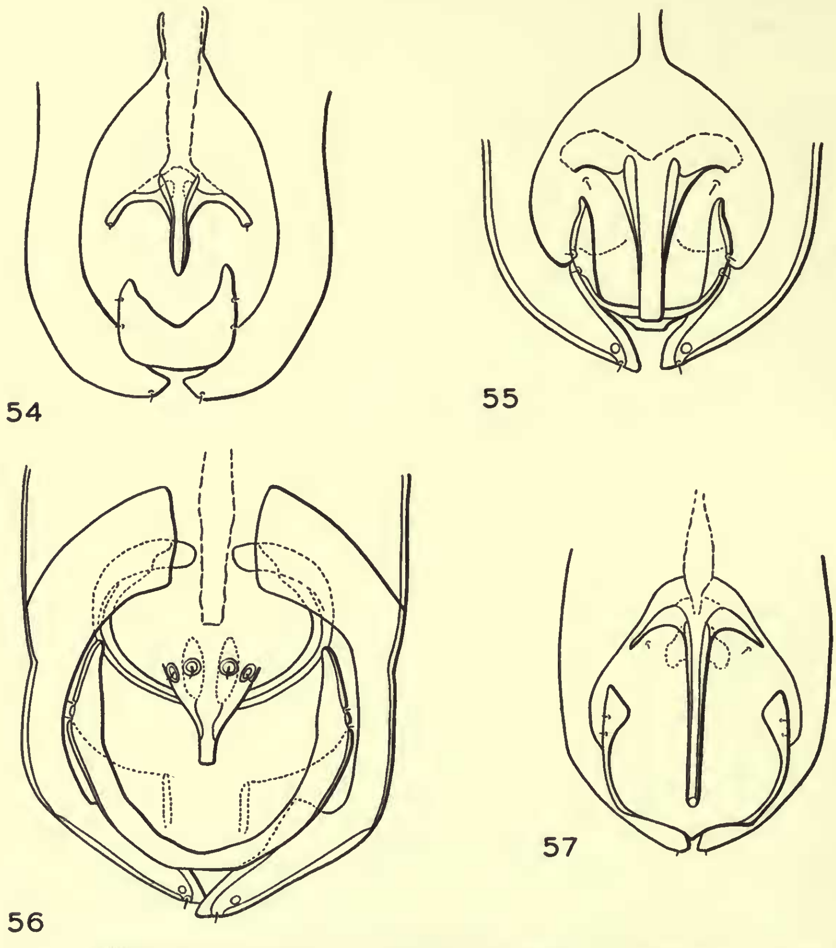
C. Specimens from *Aquila clangula* and *A. wahlbergi*.

D

	Male			*Female*
	Length	Breadth		Breadth
Head	0·50–0·58	0·38–0·47	.	0·40–0·50
Prothorax	—	0·23–0·30	.	—
Pterothorax	—	0·38–0·48	.	—
Abdomen	1·00–1·32	0·48–0·67	.	—
Total	1·75–2·23	—	.	—
C.I.	0·75–0·81	—	.	—

D. Maximum and minimum measurements of specimens from *Buteo* species.

populations from one host species to be used for taxonomic divisions. These are: exact curvature of the anterior margin of the head and thickness of the marginal carinae, both these characters also seem to be affected by the method of treatment (see p. 140); outline of gular plate and thoracic sternal plates and the number of associated setae (Text-figs. 112–118); shape and extent of unsclerotized area of tergite II; central narrowing of fused tergite IX–X in male; outline of male genital plate; exact outline of basal apodeme, differences in its total length and ratio of its length to that of the mesosome; shape of penial arms; ratio of height to breadth of female genital plate and exact outline of subvulval sclerites. Pl. 1, figs. 1–7, show the variation in the shape of the head of specimens from various hosts; figs. 3–4 are specimens from the same host individual and mounted on the same slide. As already discussed above (p. 134) there is a tendency for the populations on larger host species to have a greater number of larger individuals. This is true of the populations from the species of *Buteo* : measurements of head breadth of 321 males from 17 forms of *Buteo* and 396 females from 16 forms show a difference in the average breadth of the head between some of these populations. Thus, in males (53 specimens) from *Buteo buteo* (the smaller bird) the average is 0·41 mm., while in those



FIGS. 54–57.—Male genitalia, ventral view of distal area. 54. *D. elani*. 55. *D. rufa* from *F. tinnunculus*. 56. *D. r. regalis* from *Milvus milvus*. 57. *D. punctifer*.

(41 specimens) from *Buteo jamaicensis borealis* (the larger bird) the average is 0·44 mm. Populations from other species of *Buteo* have intermediate averages and there is overlap in measurements of individuals of all populations. In addition to size some of the populations are composed of individuals in which the head tends to be more rounded anteriorly, such as that from *Buteo jamaicensis* (Pl. 1, fig. 7), although even in this case there are individuals indistinguishable from those from other

hosts. For these reasons it has not been found possible to recognize taxonomically the populations from the different species of *Buteo* and to separate these from the populations from *Aquila* ; this is also true of the population parasitic on *Geranoaetus.*

There are considerable difficulties in placing the populations from the following hosts : *Ichthyophaga, Polemaëtus, Lophaëtus, Hieraaëtus,* and *Spilornis.* Specimens from *Ichthyophaga* and *Polemaëtus* can probably be included with *fulva,* but the available material is not in sufficiently good condition for exact comparison. Those from *Lophaëtus* and *Hieraaëtus* are rather similar and have the anterior inner margin of the marginal carina sloping posterolaterally instead of being nearly parallel with the anterior margin as in typical *fulva* ; however in some specimens the difference is less marked and a similar condition is found in some specimens from *Aquila wahlbergi.* In the specimens from *Hieraaëtus* the shape of the penial arms differ slightly from those of typical *fulva,* but in *Lophaëtus* both types occur. The population from *Melierax musicus poliopterus* resembles that from *Lophaëtus* in the characters of the margin carina, but specimens from some subspecies of *Melierax metabates* are intermediate between the latter and *fulva.* Specimens from *Spilornis* resemble the *Lophaëtus* population but have a broader head anteriorly and may differ in colour pattern but the material is not in sufficiently good condition for identification. Nymphs are available from the *Melierax metabates* population only ; these resemble those from *Buteo.* Taking all these facts into consideration it does not seem that at the present time the classification will be simplified by giving subspecific names to all these poorly separable, perhaps inseparable, populations (see above p. 138) and these are, therefore, here kept for the present under the name *fulva.*

The material available from *Melierax* is confusing : as shown above that from *M. musicus poliopterus* (5 ♂ from 3 individuals from Kenya) and that from some forms of *M. metabates* ((11 ♂ from Portugese E. Africa, Aden (1,000 ♂ and 2,068 ♀ in spirit), Morocco and SW. Africa)) are near *fulva* while 9 ♂ from *M. gabar* and 7 ♂ from *M. metabates* from two individuals from Uganda differ constantly in the characters of the male genitalia and cannot be included in *fulva.* Specimens from *Hypomorphus urubitinga* belong to the *fulva* species group but seem to differ in the details of the male genitalia but the available material is not in sufficiently good condition for a decision on this.

Material examined. Three ♂, 6 ♀ from *Aquila chrysaëtos* (Linn.), Portugal ; 3 ♀ from *Aquila heliaca* Savigny, Kurdestan ; 2 ♀ from *Aquila rapax* (Temminck), Rajputana and Kenya ; 3 ♂, 5 ♀ from *Aquila clanga* Pallas, Czechoslovakia and Germany ; 4 ♂, 5 ♀ from *Aquila verreauxii* Lesson, Rondebosch, South Africa ; 7 ♂, 7 ♀ from *Aquila wahlbergi,* Sundevall, Uganda ; 1 ♂, 8 ♀ from *Aquila pomarina* Brehm, no data. Many males and females from the following forms of *Buteo* : *B. rufinus rufinus* (Cretzschmar), *B. rufinus cirtensis* (Levaillant), *B. rufofuscus* (R. J. Forster), *B. r. augur* Rüppell, *B. hemilasius* Temminck & Schlegel, *B. regalis* (G. R. Gray), *B. jamaicensis alascensis* Grinnell, *B. j. borealis* (Gmelin), *B. j. kriderii* Hoopes, *B. j. costaricensis* Ridgway, *B. harlani* (Audubon), *B. l. lineatus* (Gmelin), *B. b. buteo* (Linn.), (including holotype, allotype and paratypes of *D. giebeli* Hopkins), *B. v. vulpinus* (Gloger), *B. b. burmanicus* Hume, *B. l. lagopus* (Pontoppidan), *B. l. s.-johannis* (Gmelin). Four ♂, 25 ♀ from *Geranoaetus melanoleucus australis* Swan, Chile. Eighteen ♂, 25 ♀ from *Icthyophaga ichthyaetus ichthyaetus* (Horsfield), Deccan, India. Eight ♂, 7 ♀ from *Lophaëtus occipitalis* (Daudin), Sudan, Uganda, Kenya.

Seven ♂, 7 ♀ from *Hieraaëtus ayresii* (Gurney), Uganda; 1 ♂, 1 ♀ from *H. pennatus* (Gmelin), Palestine. Sixteen ♂, 38 ♀ from *Spilornis cheela albidus* (Temminck), Rajputana; 2 ♂, 1 ♀ from *Spilornis c. cheela* (Latham), Nepal, 2 ♂, 1 ♀ from *Spilornis c. burmanicus* Swan, Thailand. Nine ♂, 7 ♀ from *Polemaëtus bellicosus* (Daudin), Natal and Zoo. Five ♂, 16 ♀ from *Melierax musicus poliopterus* Cabanis, Kenya; 11 ♂, 5 ♀ from *Melierax metabates* subspp. from Aden, Morocco, SW. Africa, Portugese E. Africa.

Degeeriella rima sp. n.

Type host: *Kaupifalco monogrammicus* (Temminck)

(Text-figs. 101, 123)

This subspecies is distinguished from *fulva* by the head being narrower and more rounded anteriorly (Text-fig. 123), by the pleural thickening of at least some of the segments having the ventral outline rounded and in the male by having a definite lateral slit each side of the basal apodeme (Text-fig. 101). This last character should not be confused with a displacement of the lateral thickening of the basal apodeme at the usual slight interruption of this thickening, which may be found in any of the species.

MATERIAL EXAMINED. Eleven ♂, 8 ♀ from the type host from Uganda and N. Rhodesia.

Holotype male and *allotype* female, slide No. 629 in the British Museum from *Kaupifalco monogrammicus* (Temminck) from Bunyoro, Uganda collected by W. J. Eggeling, 4.iv.1940 and presented by G. H. E. Hopkins. *Paratypes*: 10 ♂, 7 ♀ from the same host species with data as given above.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (10)	0·49–0·53	0·52	0·37–0·40	0·38
Prothorax (2)	—	—	0·23–0·25	—
Pterothorax (2)	—	—	0·38–0·40	—
Abdomen (2)	0·97–1·02	—	0·51–0·52	—
Total (2)	1·73–1·83	—	—	—
Genitalia (1)	0·34	—	—	—
C.I. (10)	0·72–0·77	0·74	—	—

Female

	Length		Breadth	
	Range	Mean	Range	Mean
Head (8)	0·53–0·59	0·57	0·40–0·45	0·42
C.I. (8)	0·735–0·775	0·76	—	—

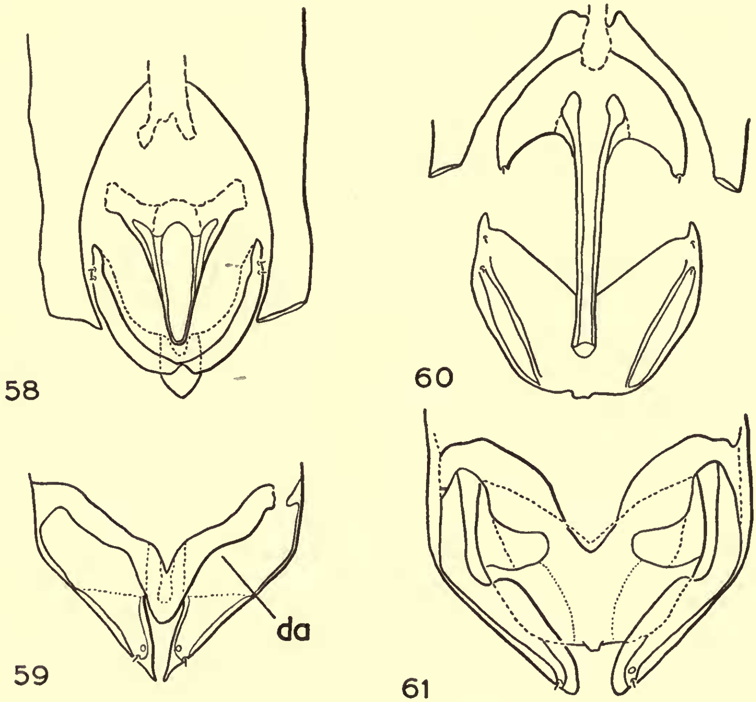
Degeeriella africana sp. n.

Type host : *Stephanoaëtus coronatus* (Linn.)

(Pl. 2, fig. 1 ; text-fig. 85)

This form is distinguished from *fulva* by the shape of the head and marginal carina and the absence of a pleural seta on segment V.

MALE. Head with inner dorsal edge of marginal carina indented medially, ventral suture reaches to anterior margin of head. Tergum II with median indentation,



FIGS. 58–61. Male genitalia. 58–59.—*D. guimarãesi*. 58. Ventral. 59. Dorsal. 60–61.—*D. meinertzhageni*. 60. Ventral. 61. Dorsal. *da*.—dorsal endomeral arm.

III with small median concavity of varying depth. Width of pleural thickening as in *fulva*, but that of segment VII has a smaller re-entrant head. Genitalia as in *fulva*, except that on the available material the sides of the basal apodeme appear to be straighter.

FEMALE. Terga of IX–XI as in *fulva*. Genital plate relatively broader in the anteroposterior line and subvulval sclerites shorter and blunter (Text-fig. 85).

CHAETOTAXY OF ABDOMEN. As in *fulva* except that tergocentral setae of III–V are normally 6, range 5–8, and there is no pleural seta each side of V.

MATERIAL EXAMINED. Six ♂, 8 ♀ from *Stephanoaëtus coronatus* (Linn.), Nairobi, Kenya, 5.ii.1917 (skin in Nairobi Museum) collected by G. H. E. Hopkins.

Holotype male and *allotype* female, slide no 624 in the British Museum (Natural History) from *Stephanoaëtus coronatus* with data as given above, presented by Mr. G. H. E. Hopkins. *Paratypes* : 5 ♂, 7 ♀ from the same host individual.

Measurements in mm.

Male

(5)

	Length		Breadth	
	Range	Mean	Range	Mean
Head	0·58–0·60	0·58	0·47–0·48	0·47
Prothorax	—	—	0·28–0·33	0·32
Pterothorax	—	—	0·47–0·50	0·49
Abdomen	1·20–1·33	1·25	0·60–0·67	0·62
Total	2·12–2·31	2·20	—	—
Genitalia (1)	0·43	—	—	—
C.I.	0·79–0·82	0·80	—	—

Female

	Length		Breadth	
	Range	Mean	Range	Mean
Head (7)	0·60–0·63	0·62	0·48–0·52	0·50
Prothorax (8)	—	—	0·31–0·35	0·33
Pterothorax (8)	—	—	0·49–0·55	0·52
Abdomen (6)	1·22–1·50	1·37	0·63–0·70	0·67
Total (6)	2·17–2·53	2·33	—	—
C.I. (7)	0·79–0·83	0·81	—	—

Degeeriella beaufacies Ansari, 1955

Type Host : *Butastur teesa* (Franklin)

(Pl. 8, fig. 4 ; Text-figs. 2, 23, 43, 77)

Degeeriella beaufacies Ansari, 1955. *Proc. VIIth Pakistan Sci. Conf.*, Biol. : 43. Host : *Butastur teesa.*

Degeeriella beaufacies Ansari, 1956. *Indian Journ. Entom.* **17** : 395 (1955). Host : *Butastur teesa.*

It is being assumed that the specimens available from *Butastur teesa* are this species, although in the first reference the few words of description do not distinguish the species from any other *Degeeriella*, and the second reference, in which the species is also referred to as new, is even less informative.

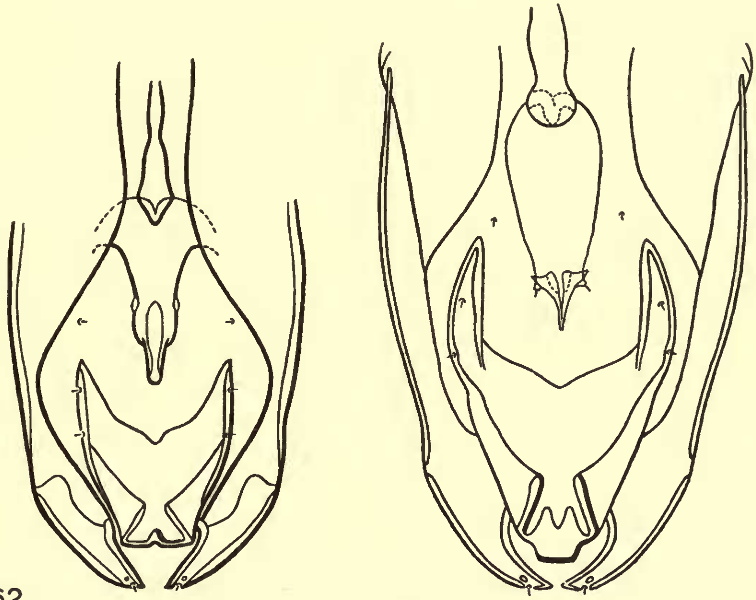
This species is distinguished from *fulva* by the form of the ventral suture, internal and external male genitalia and the nymphs.

MALE. Shape of head similar to that of *fulva*, anterior margin varies from flattened to somewhat rounded ; ventral suture does not reach anterior margin of head ; marginal carinae of temples as in *fulva*. Tergites and pleurites as in *fulva*. Genitalia differ from those of *fulva* in details of the mesosome (Pl. 8, fig. 4, Text-fig. 43). Internal genitalia as in Text-fig. 2.

Female. Terga of segments IX–XI and genital region as in *fulva*, but inner genital sclerites somewhat narrower (Text-fig. 77).

Measurements. These fall within the range for specimens of *D. fulva* from *Buteo* species. The measurements given by Ansari for the types of *beaufacies* are markedly smaller.

Chaetotaxy of abdomen. As in *fulva* but the total number of marginal setae on the last segment of the male varies from 11–17. One female has 2 tergocentral setae on the anterior margin of IX as in *discocephalus*.



62

63

Figs. 62–63. Male genitalia, ventral view of distal area.
62. *D. phlyctopygus*. 63. *D. mookerjeei*.

Nymphs. Third instar nymphs differ from those of *fulva* in having the preantennal region narrowed to a greater extent anteriorly and somewhat pointed (Text-fig. 23).

Material examined. Eighty-one ♂, 65 ♀ from *Butastur teesa* from various localities in India ; 1 ♂ from *Butastur liventer* (Temminck) from Burma.

Degeeriella carrikeri sp. n.

Type host : *Leucopternis polionota* Kaup.

(Pl. 2, fig. 2, Text-figs. 27, 44, 86)

This species is distinguished from *fulva* by the sculpturing of the dorsal surface of the head, pleural thickening and details of the male genitalia.

Male. Head similar to that of *fulva*, but flattened anteriorly with slight median concavity ; inner margin of marginal carina with median indentation ; dorsal sculpturing more marked and forming semicircular patch near anterior margin of head; ventral suture passes nearly to anterior margin and is broad anteriorly; marginal carinae of temples as in *fulva*. Tergites as in *fulva*. Pleural thickening broader than in *fulva*, with ventral outline of segments III–VII and dorsal outline of segments V–VII convex. Genitalia differ from those of *fulva* in the shape of the basal apodeme and details of mesosome.

FEMALE. Terga of IX–XI and genital region as in *fulva* except for the shape of the subvulval sclerites (Text-fig. 86).

CHAETOTAXY OF ABDOMEN. As in *fulva* except for the smaller number of tergocentral setae on segments II–V: II normally 4, range 3–5, III–V normally 6, range 4–7. In the male total number of marginal setae on last segment varies from 13–18.

MATERIAL EXAMINED. Fifteen ♂, 11 ♀ from *Leucopternis polionota* Kaup from S. Paulo, Brazil collected by S. Lima, November, 1949.

Holotype male and *allotype* female in the collection of Dr. L. R. Guimarães from *Leucopternis polionota* with the above data. *Paratypes*: 14 ♂, 10 ♀ from the same host individual.

Named in honour of Mr. M. A. Carriker.

Measurements in mm.

	Length		Breadth	
	Range	Mean	Range	Mean
Male				
Head (15)	0·60–0·62	0·61	0·46–0·49	0·47
Prothorax (10)	—	—	0·31–0·35	0·33
Pterothorax (10)	—	—	0·45–0·53	0·48
Abdomen (10)	1·13–1·27	1·19	0·58–0·65	0·60
Total (10)	2·15–2·30	2·19	—	—
Genitalia (3)	0·408–0·412	—	—	—
C.I. (15)	0·770–0·795	0·786	—	—
Female				
Head (10)	0·62–0·67	0·65	0·48–0·52	0·51
C.I. (10)	0·790–0·815	0·796	—	—

Degeeriella emersoni sp. n.

Type host: *Buteogallus gundlachii* (Cabanis)

(Text-figs. 28, 45, 78, 87)

This species is distinguished from *fulva* by the form of the marginal carina, pleural thickening and male genitalia.

MALE. Head with general outline as in *fulva*, but anterior margin of marginal carina flattened and slightly concave medially; inner margin of marginal carina indented medially; ventral suture reaches to or nearly to anterior margin of head; marginal carinae of temples as in *fulva*. Abdominal tergites as in *fulva*. Pleural thickening ventrally as in *fulva*, that is narrow with straight margin ; dorsal outline broader and curved. Genitalia similar to those of *fulva*, but differ in details of penial arms and endomeral plate.

FEMALE. Terga of IX–XI and genital region as in *fulva* ; genital plate and subvulval sclerites as in Text-figs. 78, 87.

CHAETOTAXY OF ABDOMEN. Tergocentral setae with range as in *fulva*, but segments II–V normally have 6–7 rarely 8. Pleural and sternal setae as in *fulva*. In the male the total number of marginal setae of the last segment varies from 11–15.

Measurements fall within the range as given for specimens from *Buteo lagopus* (see table).

MATERIAL EXAMINED. Twenty-three ♂, 34 ♀ from *Buteogallus gundlachii* Cabanis from Doce Legues, Cuba (collected by H. S. Peters). 4 ♂, 3 ♀ in rather poor condition from *Parabuteo unicinctus* (Temminck) seem to belong to this species.

Holotype ♂ and *allotype* ♀ in U.S. Bureau of Entomology, Washington from *Buteogallus gundlachii* with data as above. *Paratypes* : 22 ♂, 33 ♀ from the same host individual.

This species is named in honour of Dr. K. C. Emerson.

Degeeriella nisus (Giebel)

Specimens of *Degeeriella* have been seen from only nine species of *Accipiter* out of the 44 listed by Peters (1931), but even this small number shows more diversity in the populations from the different host species than in the case of the populations from *Buteo*. Four forms are here recognized and placed as subspecies of *nisus*, although when a greater amount of material is available from *Accipiter* it may be necessary to recognize some of the populations as species. For instance, *haydocki* and *frater* are rather different from *nisus* and *vagans* and could perhaps be considered as specifically distinct. It should be noted that there tends to be some variation in the outline of the endomeral plate.

Degeeriella nisus nisus (Giebel), 1866

Type host : *Accipiter n. nisus* (Linn.)

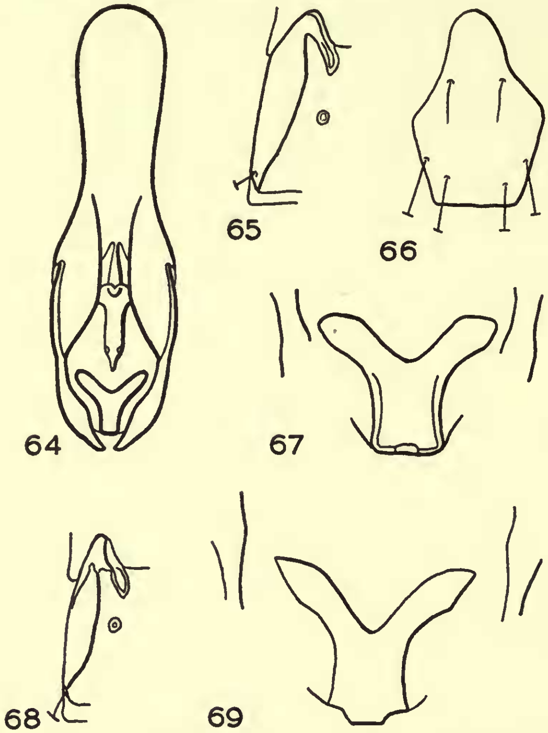
(Pl. 3, fig. 1 ; Pl. 8, fig. 5 ; Text-figs. 24, 29, 46, 88, 110)

Nirmus nisus Giebel, 1866. *Z. ges. NatWiss.* **28** : 364. Host : *Astur nisus* = *Accipiter n. nisus* (Linn.).

This species is distinguished from *fulva* by the shape of the head, the form of the marginal carina, the pleural thickening and the details of the male genitalia and from *fusca* as given under that species.

MALE. Inner edge of marginal carina straight or with slight median indentation ; small area of dorsal thickening immediately below marginal carina ; ventral suture does not reach to anterior margin of head (Text-fig. 110). Marginal temporal carinae broad with many indentations. Terga II–III indented medially. Pleural thickening broad with ventral outline convex. Genitalia similar to those of *fulva* but differ in detail (Pl. 8, fig. 5; Text-figs. 29, 46); there is some variation in the shape of the dorsal endomeral and penial arms. Internal genitalia, represented by one example in rather poor condition, appear to be the same as those of *D. fulva* from *Buteo buteo*.

FEMALE. Abdominal terga of IX–X as in fulva. Genital region similar to that of *fulva*; subvulval sclerites as in Text-fig. 88.



FIGS. 64–69.— 64–67.—*D. phlyctopygus*. 64. Male genitalia. 65. Pleural thickening of segment IV. 66. Male thoracic sternal plate. 67. Dorsal arms of endomeral plate. 68–69.—*D. mookerjeei*. 68. Pleural thickening of segment IV. 69. Dorsal arms of endomeral plate.

CHAETOTAXY OF ABDOMEN. Tergocentral setae: II normally 4, range 3–5; III–VI normally 6, range 4–7, VIII range 4–6; X in the male with 1 seta each side (58 specimens examined), in the female 2 each side; in the male total number of marginal setae, dorsal and ventral on last segment varies from 5–12. Pleural and sternal setae as in *fulva*.

NYMPHS. Anterior margin of head of third instar rather less flattened than in adult (Text-fig. 24).

MATERIAL EXAMINED. Sixty-six ♂, 113 ♀ from various subspecies of *Accipiter nisus* (Linn.) from the British Isles, Hungary, Cyprus, Saudi Arabia, Afghanistan and

Pakistan. Two ♂, 4 ♀ from *Accipiter striatus velox* (Wilson) from British Columbia and U.S.A. are included under *nisus nisus*, although in the small number of specimens available the marginal temporal carinae are somewhat narrower.

Neotype of *Nirmus nisus* Giebel: Male, slide no. 627, in the British Museum (Natural History) from *Accipiter n. nisus* (Linn.) from Kildare, Ireland, presented by Mr. G. H. E. Hopkins.

Degeeriella nisus vagans (Giebel), 1874

Type host: *Accipiter gentilis* (Linn.)

(Pl. 3, fig. 2)

Nirmus vagans Giebel, 1874. *Insecta epizoa*: 126. Host: *Astur palumbarius* = *Accipiter gentilis* (Linn.).

This differs from the nominate form in the larger average size of both sexes, the shape of the head, the inner edge of the marginal carina, which is usually rather more indented medially, the narrower and less indented marginal carinae of the temples and the number of tergocentral setae. Tergocentral setae: II normally 6 (rarely 5 or 8, often 7); III–V normally 8; VI–VIII normally 6; thus in *nisus* the total number of tergocentral setae on segments III–V is 15–20, normally 18 and in *vagans* 22–26, normally 24.

NYMPHS. Third instar nymphs with head similar to those of *nisus nisus*, but differ slightly reflecting the differences in the adult heads.

MATERIAL EXAMINED. Forty-one ♂, 44 ♀ from *Accipiter gentilis* (Linn.) from Germany, Switzerland, Czechoslovakia, Canada and Alaska. Fourteen ♂, 48 ♀ from *Accipiter cooperii* (Bonaparte) from United States of America and British Columbia are not separable from *vagans*.

Neotype of *Nirmus vagans* (Giebel), 1874: Male, slide no. 628 in the British Museum (Natural History) from *Accipiter gentilis* from Rheinfelden, Switzerland, 15.ii.1943 presented by Mr. G. H. E. Hopkins.

Measurements in mm.

Male

D. n. nisus

	Length		Breadth	
	Range	Mean	Range	Mean
Head (50)	0·45–0·52	0·49	0·33–0·39	0·36
Prothorax (10)	—	—	0·22–0·25	0·23
Pterothorax (10)	—	—	0·33–0·38	0·36
Abdomen (10)	0·90–1·10	0·99	0·42–0·53	0·48
Total (10)	1·56–1·87	1·72	—	—
Genitalia (2)	0·29–0·31	—	—	—
C.I. (50)	0·73–0·79	0·76	—	—

Male

D. n. vagans

Head (12)	0·52–0·56	0·54	0·39–0·43 (30)	0·42
Prothorax (10)	—	—	0·27–0·29	0·28
Pterothorax (11)	—	—	0·42–0·47	0·44
Abdomen (10)	1·05–1·17	1·11	0·55–0·59	0·57
Total (10)	1·83–2·00	1·94	—	—
Genitalia (1)	0·32	—	—	—
C.I. (12)	0·77–0·80	0·79	—	—

Female

D. n. nisus

Head (10)	0·52–0·57	0·54	0·37–0·42 (30)	0·40
Prothorax (10)	—	—	0·22–0·27	0·26
Pterothorax (10)	—	—	0·37–0·43	0·41
Abdomen (10)	1·13–1·36	1·27	0·45–0·58	0·54
Total (10)	1·91–2·23	2·09	—	—
C.I. (10)	0·73–0·78	0·75	—	—

Female

D. n. vagans

Head (12)	0·57–0·58	0·57	0·42–0·46 (30)	0·45
Prothorax (10)	—	—	0·28–0·32	0·30
Pterothorax (10)	—	—	0·47–0·49	0·48
Abdomen (10)	1·21–1·35	1·30	0·57–0·63	0·62
Total (10)	2·07–2·25	2·19	—	—
C.I. (12)	0·74–0·81	0·78	—	—

Degeeriella nisus frater (Piaget), 1880

Type host (emended) : *Accipiter badius* (Gmelin)

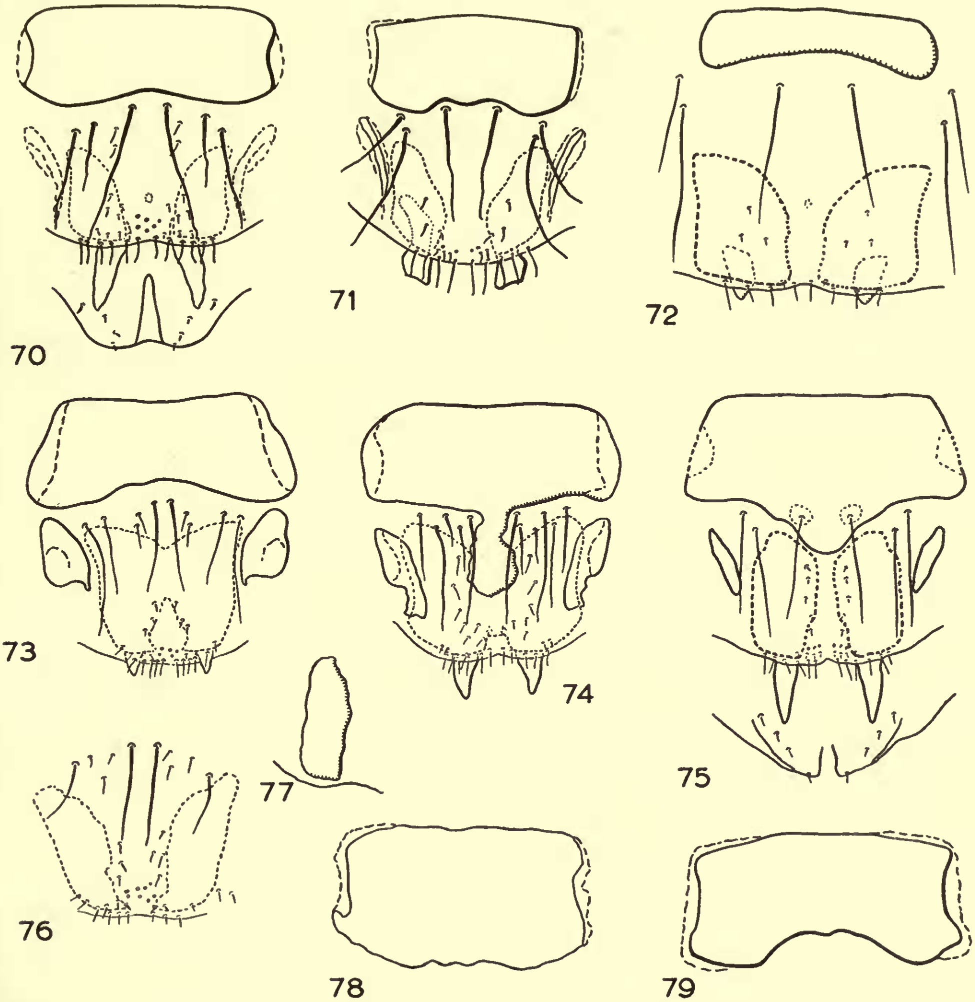
(Pl. 3, fig. 3 : Text-figs. 25, 31–32, 47)

Nirmus frater Piaget, 1880. *Pediculines* : 145, pl. 12, fig. 2. Host : *Lamprotornis amethystina.* Error.

Nirmus frater is represented in the Piaget collection by a single male labelled as from the original host with " Habesh " in brackets, perhaps Habesh in N. Syria. It has not been possible to separate specimens from *Accipiter badius* (African and Syrian birds, see below) from the type of *frater* (although exact comparison of the male genitalia is not possible) and it is presumed that this bird was the original host.

This subspecies is distinguished from the nominate form by the shape of the head, by the slight concavity of the central part of the outer edge of the marginal carina, by the rather larger dorsal central thickening below the marginal carina, by the narrower and more curved penial arms and the shape of the endomeral plate. There is, however, some variation in this last character (Text-figs. 31–32). Tergum II does not have a narrow median indentation as is usual in *nisus*, but a shallow concavity which is sometimes hardly visible ; tergum III and chaetotaxy of the abdomen as in *nisus*.

NYMPHS. Second and third stage nymphs have been seen from *A badius poliopsis* and third stage from *A. virgatus affinis*, these resemble each other and differ from



FIGS. 70–79. 70–76.—Female genital regions. 70. *D. fulva* from *Aquila chyrsaëtos*. 71. *D. hopkinsi*. 72. *D. d. discocephalus*. 73. *D. meinertzhageni*. 74. *D. guimarãesi*. 75. *D. rufa*. 76. *D. elbeli*. 77. Inner genital sclerite of *D. beaufacies*. 78–79.—Female genital plates. 78. *D. emersoni*. 79. *D. leucopleura*.

those of *Degeeriella n. nisus* and *D. n. vagans* in having the anterior margin of the head more pointed and a larger thickened area anteriorly.

Specimens have been seen from subspecies of *Accipiter badius* from Syria, Somaliland, Uganda, Kenya, Nepal and Thailand. Those from the Thailand birds (*A.*

badius poliopsis) tend to differ from those from the Syrian and African birds in having the outer edge of the marginal carina somewhat more concave medially and in having none or very few indentations in the inner edge of the marginal carina laterally. The specimens from Nepal resemble those from Thailand in the form of the anterior margin of the head and the African specimens in the lateral indentations of the, marginal carina. However, there are individuals from all these localities which are indistinguishable from each other ; it does not seem reasonable, therefore, to disguish taxonomically the populations from these different subspecies of *Accipiter badius*. There is also some variation in the shape of the dorsal endomeral arms.

MATERIAL EXAMINED. One ♂ type of *Nirmus frater* ; males and females from *Accipiter badius* (Gmelin) from Syria (1 ♂, 3 ♀), from Africa (Uganda, Kenya, Somaliland, 14 ♂, 26 ♀), from Nepal (23 ♂, 27 ♀), from Burma (7 ♂, 10 ♀) and Thailand (9 ♂, 14 ♀). Three ♂, 8 ♀ from *Accipiter tachiro* (Daudin) from Uganda and S. Africa. One ♂, 4 ♀ from *Accipiter virgatus affinis* Hodgson from Thailand and 2 ♂, 3 ♀ from *A. virgatus gularis* (Temminck & Schlegel) from Thailand.

Lectotype of *Nirmus frater* Piaget : ♂ (slide no. 1270) in the Piaget collection, British Museum (Natural History).

Measurements in mm.

Lectotype (♂) *of* frater

	Length	Breadth
Head	0·57	0·43
Prothorax	—	0·29
Pterothorax	—	0·47
Abdomen	1·18	0·58
Total	2·03	—
Genitalia	0·33	—
C.I.	—	—

Breadth of Head of Male Specimens from Accipiter badius

East Africa (11)		Nepal (22)		Thailand (10)	
Range	Mean	Range	Mean	Range	Mean
0·38–0·42	0·40	0·38–0·43	0·42	0·38–0·40	0·39

Degeeriella nisus haydocki subsp. n.

Type host : *Accipiter minullus* (Daudin)

(Pl. 2, fig. 3)

This form is separated from the other known subspecies of *nisus* with the exception of *epustulata* by having only four tergocentral setae on segments II–VIII. It is separated from this latter species by the size and shape of the head. It resembles *frater* in the characters of the anterior margin of the marginal carina ; in having a dorsal triangular-shaped thickening below the marginal carina, which is rather larger ; in the form of tergum II and in the shape of the penial arms.

MATERIAL EXAMINED. Nine ♂, 11 ♀ from *Accipiter minullus* (Daudin) from Gulu, Uganda and N. Rhodesia.

Holotype male and *allotype* female, slide no 625 in the British Museum (Natural History). from *Accipiter minullus*, Mulashi, N. Rhodesia, 27.vi.1955 collected by Major E. L. Haydock. Paratypes : 8 ♂, 10 ♀ from the same host species with data as given above.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (9)	0·49–0·53	0·50	0·35–0·37	0·360
Prothorax (7)	—	—	0·24–0·26	0·250
Pterothorax (7)	—	—	0·37–0·39	0·375
Abdomen (7)	0·95–1·05	0·97	0·46–0·50	0·475
Total (7)	1·71–1·83	1·75	—	—
Genitalia (2)	0·325–0·330	—	—	—
C.I. (9)	0·69–0·73	0·71	—	—

Female

	Length		Breadth	
	Range	Mean	Range	Mean
Head (10)	0·53–0·57	0·55	0·37–0·42	0·39
Prothorax (8)	—	—	0·26–0·28	0·27
Pterothorax (8)	—	—	0·40–0·43	0·42
Abdomen (8)	1·17–1·27	1·21	0·52–0·57	0·53
Total (8)	2·00–2·10	2·03	—	—
C.I. (10)	0·68–0·74	0·71	—	—

Degeeriellia nisus epustulata (Carriker), 1903

Type host : *Accipiter bicolor* (Vieillot)

(Text-fig. 124)

Nirmus fuscus epustulatus Carriker, 1903. *Univ. Nebr. Stud.* **3** : 133. Host : *Accipiter bicolor*.

Through the kindness of Mr. Carriker it has been possible to examine a single female paratype of this form. It resembles *haydocki* in having only four tergal setae on each of segments III–VIII, but differs from this form in the shape of the head and the larger size.

Measurements in mm.

Female

	Length	Breadth
Head	0·60	0·47
Prothorax	—	0·30
Pterothorax	—	0·47
Abdomen	1·30	0·57
Total	2·12	—

Degeeriella fusca (Denny), 1842

Type host : *Circus ae. aeruginosus* (Linn.)

(Pl. 4, fig. 3 ; Pl. 8, fig. 6 ; Text-figs. 3, 30, 48)

Nirmus fuscus Denny, 1842. *Mon. Anopl. Brit.* : 49, 118. Host : *Circus rufus* = *Circus ae. aeruginosus* (Linn.).

Nirmus socialis Giebel, 1874. *Insecta epizoa* : 127. Hosts : *Circus cineraceus* = *C. pyargus* (Linn.), and *C. aeruginosus* (Linn.

Nirmus aeruginosi Denny, 1852. *List Brit. Animals in Brit. Mus.*, pt. 11, Anoplura : 16. *Nomen novum* for *Nirmus fuscus* Denny.

Kélerinirmus circi Boetticher & Eichler, 1954. *Biol. Zbl.* **73** : 215. Host : *Circus aeruginosus* (Linn.).

Hopkins (1947 : 76) has discussed the confusion which has arisen over the author of this name and the type host and shown that Denny must be considered as the sole author with *Circus ae. aeruginosus* as the type host.

This species resembles most nearly *D. n. nisus* from which it is distinguished by the colour pattern and details of the male genitalia.

Male. Dorsal surface of head with an area of lighter sclerotization between the anterior dorsal setae. Inner dorsal margin of marginal carina indented medially ; ventral suture as in *nisus*. Tergites II–III with median indentation ; central area of tergite II more strongly pigmented than lateral areas. Pleural thickening broad and strongly pigmented with dark inner line, contrasting with the rather lightly sclerotized terga ; this character is not so marked in specimens from *Circus cyaneus*. Genitalia similar to those of *fulva* but differ in detail. Internal genitalia as shown in Text-fig. 3.

Female. Terga of IX–XI and genital region as in *fulva*.

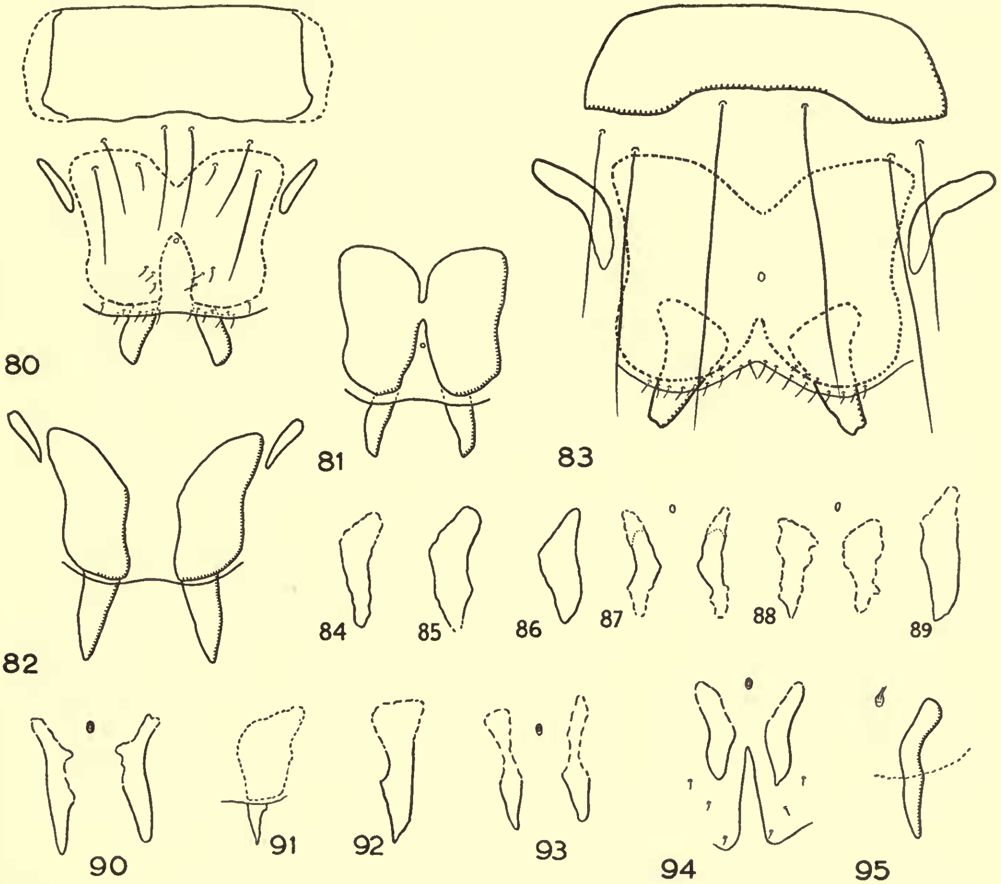
Chaetotaxy of abdomen. Tergocentral setae : II normally 6, range 5–7 ; III–IV normally 8, range 6–9 ; V normally 7–8, range 5–8 ; VI–VII normally 6, range 5–8 ; VIII normally 6, range 4–6 ; X in the male has 1 seta each side (58 examined), in the female 2 each side ; total number of marginal setae on last segment varies from 6–12. Pleural and sternal setae as in *fulva*.

Nymphs. Third instar nymphs have been seen from two host species, *Circus cyaneus* and *C. melanoleucus* ; these have the anterior margin of the head more pointed than in the adult.

Host distribution. There appear to be no taxonomically recognizable differences between the population from the five species of *Circus* listed below. Eleven specimens from one host individual of *Circus melanoleucus* average somewhat smaller (breadth of head : 0·40 mm.). Specimens from *Circus cyaneus* do not seem to have the colour pattern quite typical of *fusca*, except for the darker central area of tergum II ; it is possible that these may prove to be a distinct subspecies, but fresh material from all hosts is needed.

Material examined. Fifty-five ♂, 81 ♀ from *Circus aeruginosus* (Linn.) from Czechoslovakia, Malta, Cyprus, Saudi Arabia, India, Ceylon, Cape Colony ; 13 ♂, 37 ♀ from *Circus c. cyaneus* (Linn.) from Orkneys, Hungary and Czechoslovakia ;

10 ♂, 12 ♀ from *Circus cyaneus hudsonius* (Linn.) from British Columbia and various localities in the United States of America ; 55 ♂, 74 ♀ from *Circus pygargus* (Linn.) from Cyprus and Kenya ; 16 ♂, 24 ♀ from *Circus macrourus* (S. G. Gmelin) from N. Africa, Saudi Arabia and Aden ; 10 ♂, 9 ♀ from *Circus melanoleucus* (Pennant)



FIGS. 80–95. 80–83.—Female genital regions. 80–81.—*D. r. regalis*, to show variation ; 80 from *Milvus m. milvus* and 81 from *Milvus migrans aegyptius*. 82. *D. r. castanea*. 83. *D. punctifer*. 84–95.—Subvulval sclerites. 84. *D. fulva* from *Aquila chrysaëtos*. 85. *D. africana*. 86. *D. carrikeri*. 87. *D. emersoni*. 88. *D. n. nisus*. 89. *D. leucopleura*. 90. *D. elbeli*. 91. *D. elani*. 92. *D. tendeiroi*. 93. *D. meinertzhageni*. 94. *D. guimarãesi*. 95. *D. rufa* from *Falco tinnunculus*.

from Assam and Thailand. In the Denny collection there are 7 ♀ labelled *Nirmus fuscus* by the person responsible for mounting this collection and who rarely kept Denny's original labels. These specimens have no host label, but three of the slides have a small circular (probably original) label with what appears to be " *aeruginos* ". This must refer either to *aeruginosi*, the new name given to *fuscus* by Denny in 1852 or to the name of the host, *C. aeruginosus*. The three females so labelled together with one other are the species usually found on *C. aeruginosus*: two other females are *D. r. regalis* and presumably came from *Milvus ictinus* referred to by Denny (1842: 119) and one other female is *D. fulva* and presumably came from *Buteo lagopus* also referred to by Denny. One of the females labelled "*aeruginos*" will be selected as lectotype of *fusca*.

Lectotype: ♀, slide no. 350, in the Denny collection, British Museum (Natural History); paratypes, 3 ♀ in the same collection.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (50)	0·51–0·57	0·54	0·39–0·45	0·42
Prothorax (10)	—	—	0·25–0·28	0·27
Pterothorax (10)	—	—	0·42–0·45	0·43
Abdomen (10)	1·08–1·23	1·14	0·52–0·60	0·56
Total (10)	1·88–2·12	1·98	—	—
Genitalia (2)	0·32–0·35	—	—	—
C.I. (50)	0·75–0·81	0·78	—	—

Female

(10)

Head	0·57–0·60	0·58	0·42–0·47	0·45
Prothorax	—	—	0·28–0·31	0·29
Pterothorax	—	—	0·47–0·50	0·48
Abdomen	1·31–1·40	1·36	0·62–0·68	0·64
Total	2·22–2·42	2·28	—	—
C.I.	0·75–0·80	0·78	—	—

Degeeriella hopkinsi sp. n.

Type host: *Terathopius ecaudatus* (Daudin)

(Pl. 4, fig. 2; Text-figs. 33, 49, 71)

This species is distinguished from the rest of the *fulva* species group by the presence of a pleural seta on segment IV.

MALE. Head broad and rounded anteriorly; inner edge of marginal carina indented dorsally in mid-line; ventral suture extends to or nearly to the anterior margin. Terga II–III indented; pleural thickening narrow with re-entrant heads normal only on segment III, gradually becoming more and more reduced on the following segments. Genitalia similar to those of *fulva* but differ in detail (Text-figs. 33, 49). There is some variation in the number and position of the setae associated with the ventral arms of the endomeral plate in the five males examined: two specimens had an extra seta each side anterior to the end of the arms, one had three setae on one arm and on the other one anterior to the arm and one on the arm, one specimen was normal and in one the setae could not be seen.

FEMALE. Terga of IX–XI as in *fulva*. Genital region similar to *fulva* but genital plate narrower from side to side and the subvulval sclerites shorter with blunter ends (Text-fig. 71); there are fewer sensillae anterior to the vulval margin.

CHAETOTAXY OF ABDOMEN. Tergocentral setae: II, 6; III–V, 6–8; VI–VIII, 6; X in the male has 1–2 each side and in the female 2. Pleural and sternal setae as in *fulva* except that there is a pleural seta each side of IV.

MATERIAL EXAMINED. Five ♂, 11 ♀ from *Terathopius ecaudatus* (Daudin) from Lodwar, Kenya, 7.iv.1934 (skin in Nairobi Museum) collected by G. H. E. Hopkins.

Holotype male and *allotype* female slide no. 623 in the British Museum (Natural History) from *Terathopius ecaudatus* with data as given above, presented by Mr. Hopkins. *Paratypes*: 4 ♂, 10 ♀ from the same individual.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (5)	0·53–0·57	0·55	0·43–0·48	0·45
Prothorax (5)	—	—	0·28–0·30	0·28
Pterothorax (5)	—	—	0·43–0·49	0·47
Abdomen (4)	1·12–1·22	1·18	0·58–0·65	0·62
Total (4)	1·92–2·07	2·00	—	—
Genitalia (1)	0·38	—	—	—
C.I. (5)	0·81–0·85	0·82	—	—

Female

	Length		Breadth	
	Range	Mean	Range	Mean
Head (11)	0·53–0·59	0·57	0·45–0·50	0·47
Prothorax (7)	—	—	0·28–0·30	0·28
Pterothorax (7)	—	—	0·47–0·50	0·48
Abdomen (7)	1·18–1·28	1·25	0·60–0·63	0·62
Total (7)	2·07–2·17	2·13	—	—
C.I. (11)	0·82–0·85	0·83	—	—

Degeeriella leucopleura (Nitzsch), 1874

Type host: *Circaëtus cinerascens* J. W. Muller

(Pl. 4, fig. 1; Text-figs. 34, 50, 79, 89)

Nirmus leucopleurus Nitzsch, 1874. *In* Giebel, *Insecta epizoa*: 129. Host: *Falco brachydactylus* = *Circaëtus cinerascens* J. W. Muller.

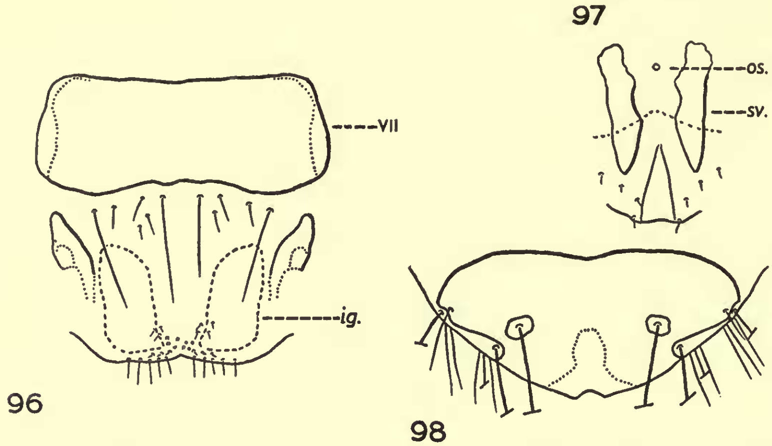
Nirmus temporalis Piaget, 1890. *Tijdschr. Ent.* **33**: 228. Pl. 8, fig. 6. Host: *Buceros manillensis*. Error.

This is a distinctive species separated by the shape of the head, form of the pleural thickening and absence of pleural seta on V.

MALE. Head broad with preantennal region rounded; inner dorsal edge of marginal carina with slight median indentation; ventral suture does not reach anterior margin. Abdomen elongated and with neither terga II nor III with a definite median slit-like indentation although II may show a slight concavity. In spite of the elongated abdomen the pleural thickening does not have the strongly sclerotized re-entrant heads characteristic of this species group. Genitalia as shown in Text-figs. 34, 50.

FEMALE. Terga of IX-XI as in *fulva*. Posterior margin of genital plate deeply emarginate and subvulval sclerites stouter than in *fulva* (Text-figs. 79, 89).

CHAETOTAXY OF ABDOMEN. Tergocentral setae: II normally 6, range 4–6; III–V normally 8, range 6–8; VI–VII normally 6, range 5–7; VII normally 4, range 3–4; X in the male with 1 each side, in female 2 each side. One female has 4 tergocentral setae on II and 6 on III–VII. Pleural setae: II–V, 0; VI–VII,



FIGS. 96–98. *Degeeriella phlyctopygus*, female. 96. Genital region. 97. Subvulval sclerites. 98. Dorsal view of segments IX–XI. *ig.*—inner genital sclerites; *os.*—opening of spermathecal tube; *sv.*—subvulval sclerite.

2 each side; VIII, 3; in the male IX has 3 and X, 0. In the female IX has 3 and X 2 each side. Sternocentral setae: II–VI normally 4, one male has 3 on VI and one female has 6 on V; in the male the last segment does not have the usual spine-like seta each side and the second seta therefore, if present, is not distinguishable from the marginal setae which total from 10–15.

NYMPHS. Second and third instars have the curvature of the anterior margin of the head similar to that of the adult; the preantennal region is shorter and the sides less straight, as is usual in nymphs.

Nirmus temporalis Piaget said to have come from *Buceros manillensis* is represented in the Piaget collection by a single male which appears to be the same as *D. leucopleura* and is presumably a straggler from *Circaëtus*.

MATERIAL EXAMINED. Four ♂, 2 ♀ from *Circaëtus cinerascens* J. W. Müller from Kapenguria, Kenya and 1 ♂ from the same host species from E. Africa (skin); 7 ♂, 11 ♀ from *Circaëtus gallicus* (Gmelin) from France, Czechoslovakia, Egypt (skin) and Cameroons (skin); 1 ♂, 1 ♀ from *Circaëtus cinereus* Vieillot from Portuguese Guinea.

Lectotype of *Nirmus temporalis* Piaget : ♂ in the British Museum (Natural History), slide no. 1421.

Neotype of *Degeeriella leucopleura* (Nitzsch) : ♂ in the Meinertzhagen collection, British Museum (Natural History), slide no. 20568 from *Circaëtus cinerascens* from Kapenguria, Kenya, March 1956.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (5)	0·65–0·67	0·66	0·52–0·53	0·52
Prothorax (5)	—	—	0·32–0·33	0·33
Pterothorax (5)	—	—	0·50–0·55	0·52
Abdomen (3)	1·32–1·43	1·38	0·65–0·68	0·67 (5)
Total (3)	2·33–2·45	2·39	—	—
Genitalia (1)	0·43	—	—	—
C.I. (5)	0·79–0·81	0·80	—	—
Female				
Head (2)	0·68–0·69	—	0·53	—
Prothorax (2)	—	—	0·35	—
Pterothorax (2)	—	—	0·53–0·55	—
Abdomen (1)	1·40	—	0·67	—
Total (1)	2·43	—	—	—
C.I. (2)	0·77–0·78	—	—	—

The discocephalus *Species Group*

1. Head index greater than 0·94.
2–3. As in *fulva* group.
4. Thoracic sternal plate as in Text-fig. 119.
5. Thorax and abdomen with shape as in Pl. 9, fig. 1.
6–7. As in *fulva* group.
8. Pleural thickening without well sclerotized re-entrant heads.
9. Sternite II in form of central triangular plate, III–VI narrow central strips of sclerotization.
10. Male genital plate small and irregular and less indented laterally than in *fulva* group.
11–13. As in *fulva* group.
14. Setae each side of posterodorsal margin of pterothorax variable in number and position.
15. Pleural setae absent on segments II–III.
16. Sternocentral setae of segments III–VI variable.
17. As in *fulva* group.

This species group is distinguished from the *fulva* group by the shape of head and abdomen ; from the *punctifer* group by the absence of head sutures and chaetotaxy of the temples, and in the females by the dorsal chaetotaxy of tergum IX and in the male by the characters of the male genitalia.

Degeeriella discocephalus discocephalus (Burmeister), 1838

Type host : *Haliaeëtus albicilla* (Linn.)

(Pl. 9, fig. 1 ; Text figs. 35, 51, 72, 106, 119)

Nirmus discocephalus Burmeister, 1838. *Handb. Ent.* **1** : 430. Host : *Aquil. albicilla* = *Haliaeëtus albicilla* (Linn.).
Nirmus discocephalus var. *amblys* Kellogg, 1896. *Proc. Calif. Acad. Sci.* (2), **6** : 499, pl. 67, fig. 6. Host : *Haliaeëetus leucocephalus* (Linn.).

The specimens used by Burmeister for his description of this species were figured by Nitzsch in Giebel, 1874 (pl. 7, fig. 10) and represent the species described below.

MALE. Marginal carina thick and entire ; ventral suture reaches to or nearly to inner margin of marginal carina. Thoracic sternal plate as in Text-fig. 119, but shows some variation in outline ; posterodorsal marginal setae of pterothorax variable in number and position, 4–6 each side (omitting the lateral spine-like seta and the seta with sunken alveolus). Tergum II with median unsclerotized area, tergum III somewhat narrowed medially. Genitalia of *fulva* type ; dorsal endomeral arms may or may not join basal apodeme.

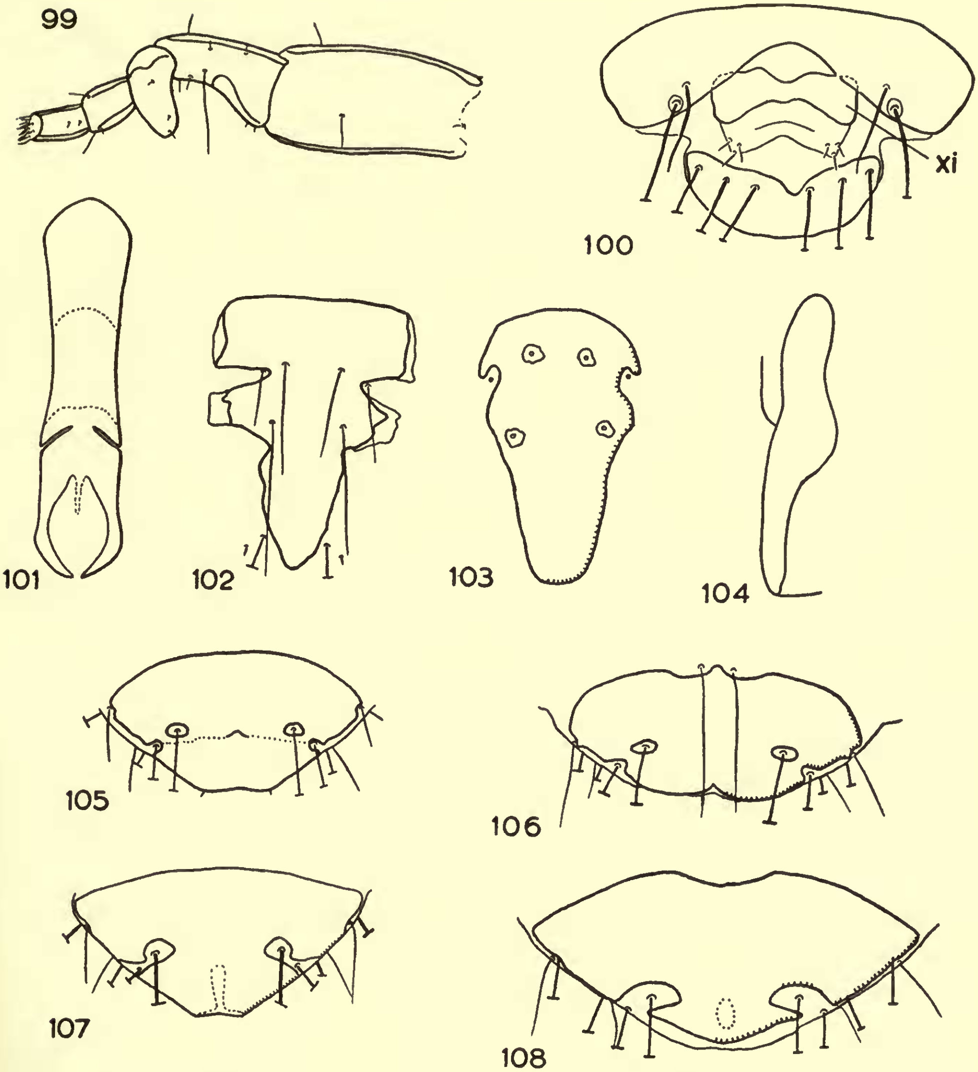
FEMALE. This species differs from all other known *Degeeriella* in having two (occasionally one) setae in the middle of the anterior region of tergite IX ; these setae are occasionally found as an abnormality in species of the *fulva* group. The subvulval sclerites are small and indistinct and almost covered by the vulva (Text-fig. 72).

CHAETOTAXY OF ABDOMEN. Tergocentral setae : II range 6–8 ; III–V, normally 8, range 6–9 ; range 6–8 ; VII–VIII normally 6, range 6–7 ; X in the male normally 2 each side, range 2–4 ; in the female IX has 2 (rarely 1) anterior setae ; X has 2 each side. Pleural setae ; II–III, 0 ; IV–V, 1 each side ; VI–VII, 2 (occasionally 1 or 3 on one side) ; VIII, 3 ; IX, 2 ; X in the male has 0 and in the female 2. Sternocentral setae irregular in number : II, 4–7 ; III–IV, 5–8 ; V, 5–7 ; VI, 4–7 ; total number of setae of segments II–VI of specimens counted varied from 24–34 ; in the male the last pair of sternal setae are both elongated. Total number of marginal setae of last segment in male varies from 12–16.

NYMPH. One third instar from *Haliaeëtus albicilla* has been seen, this resembles the adult in the shape of the head.

MATERIAL EXAMINED. Fourteen ♂, 12 ♀ from *Haliaeëtus albicilla* (Linn.) from Germany, Czechoslovakia, Finland and Russia ; 2 ♂, 5 ♀ from *Haliaeetus pelagicus* (Pallas) from Siberia ; 7 ♂, 3 ♀ from *Haliaeëtus l. leucocephalus* (Linn.) from various localities in N. America. There appear to be no constant characters on which the population (i.e. *D. amblys* (Kellogg)) found on this latter host can be separated from *discocephalus*.

Neotype of *Nirmus discocephalus* Burmeister : ♂ in the British Museum (Natural History), slide no. 617 from *Haliaeëtus albicilla* from Samorin, Czechoslovakia, 9.xii.1952.



Figs. 99–108. 99. Male antenna, *D. mookerjeei*. 100. *D. guimarãesi*, terminal segments of male abdomen. 101. *D. rima*, basal apodeme (lateral slits somewhat exaggerated). 102–103.—Male genital plates. 102. *D. fulva* from *Aquila chrysaëtos*. 103. *D. punctifer*. 104. *D. rufa* from *Falco tinnunculus*, pleural thickening of segment IV, ventral. 105–108.—Segments IX–XI of female abdomens, dorsal. 105. *D. fulva* from *Aquila chrysaëtos*. 106. *D. d. discocephalus*. 107. *D. rufa* from *F. tinnunculus*. 108. *D. punctifer*.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (11)	0·44–0·47	0·46	0·42–0·47	0·45
Prothorax (6)	—	—	0·25–0·28	0·27
Pterothorax (8)	—	—	0·35–0·43	0·40
Abdomen (7)	0·70–0·87	0·77	0·52–0·68 (8)	0·61
Total (7)	1·37–1·53	1·45	—	—
Genitalia (3)	0·42–0·44	—	—	—
C.I. (11)	0·96–1·00	0·98	—	—

Female

	Length		Breadth	
	Range	Mean	Range	Mean
Head (7)	0·50–0·53	0·51	0·50–0·53	0·52
Prothorax (6)	—	—	0·28–0·33	0·31
Pterothorax (6)	—	—	0·45–0·49	0·46
Abdomen (6)	0·97–1·13	1·05	0·68–0·77	0·73
Total (6)	1·17–1·95	1·83	—	—
C.I. (7)	1·00–1·03	1·01	—	—

Degeeriella discocephalus aquilarum Eichler, 1943

Type host : *Aquila n. nipalensis* (Hodgson)

(Pl. 9, fig. 2)

Degeeriella aquilarum Eichler, 1943. *Zool. Anz.* **142** : 92, fig. 1. Host : *Aquila n. nipalensis* (Hodgson).

This subspecies is close to the nominate form, from which it can be separated by the shape of the anterior margin of the head, the slightly better developed pleural thickening, especially on segment III and the fewer number of tergo- and sternocentral setae as follows :

	Tergocentral II–VIII		Sternocentral II–VI	
	Maximum	Minimum	Maximum	Minimum
D. d. discocephalus	52	48	34	24
D. d aquilarum	42	38	22 (1 ♀ with 31)	18

Specimens examined. Nine ♂, 8 ♀ from *Aquila n. nipalensis* Hodgson from Somaliland ; 1 ♂, 1 ♀ from *Aquila nipalensis orientalis* Cabanis, no data ; 4 ♂, 4 ♀ from *Aquila chrysaëtos* (Linn.) from Norway and Serbia ; 1 ♂, 2 ♀ from *Aquila pomarina hastata* (Lesson) from Rajputana, India and Manipur ; 8 ♂, 4 ♀ from *Aquila rapax raptor* A. E. Brehm from Somaliland ; 4 ♂, 3 ♀ from *Aquila h. heliaca* Savigny from Czechoslovakia, Egypt and Rajputana, India ; 1 ♀ from *Aquila clanga* Pallas from Russia.

There appear to be no constant differences between the populations from these species of *Aquila,* although no doubt there will be found some differences in average sizes when larger numbers are available.

Measurements in mm.

Specimens from Aquila n. nipalensis

Male

(9)

	Length		Breadth	
	Range	Mean	Range	Mean
Head	0·44–0·47	0·45	0·43–0·47	0·45
Prothorax	—	—	0·25–0·27	0·26
Pterothorax	—	—	0·38–0·42	0·40
Abdomen	0·81–0·93	0·89	0·55–0·67	0·62
Total	1·45–1·63	1·56	—	—
C.I.	0·96–1·02	0·99	—	—

The elani *Species Group*

1–5. As in *fulva* group.

6. As in *fulva* group : *elbeli* and *tendeiroi.* Tergal plates of segment XI apparent in male : *elani, meinertzhageni, guimarãesi.*

7. As in *fulva* group : *elbeli, tendeiroi* and *guimarãesi.* As in *rufa* group : *elani* and *meinertzhageni.*

8–9. As in *fulva* group.

10. As in *fulva* group : *elbeli.* Male genital plate laterally indented to a greater extent : *elani, tendeiroi, meinertzhageni* and *guimarãesi.*

11. As in *fulva* group : *elbeli, elani, tendeiroi, meinertzhageni.* Female genital plate with median prolongation : *guimarãesi.*

12. As in *fulva* group : *elbeli, elani, tendeiroi.* Inner genital sclerites fused : *meinertzhageni* and *guimarãesi.*

13. As in *fulva* group : *elbeli, elani, tendeiroi.* Distinctive types : *meinertzhageni* and *guimarãesi.*

14. As in *fulva* group.

15. Pleural setae absent on segments II–IV : *elbeli.* Pleural setae absent on segments II–V : *elani, tendeiroi, meinertzhageni, guimarãesi.*

16–17. As in *fulva* group.

It is apparent that these five species do not form a very homogeneous group and are here placed together mainly on the form of the ventral carinae which show a greater development anteriorly than those of any other species groups ; this character is more marked in *meinertzhageni* and *guimarãesi* than in the others. Apart from this character *elbeli* and perhaps *tendeiroi* could be included in the *fulva* group ; the rest of the species share some rather distinctive characters ; *guimarãesi* has certain characters found elsewhere only in *rufa.* It is possible that these five species do not, in fact, form a related group.

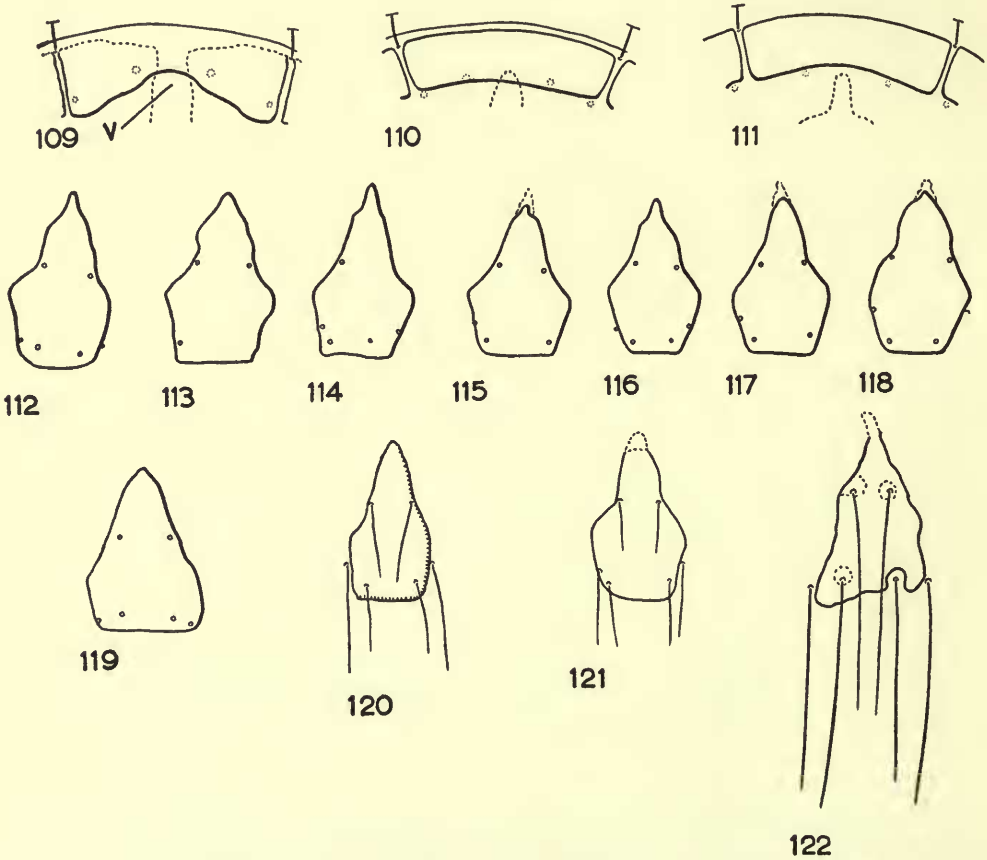
Degeeriella elbeli Clay, 1958

Type Host : *Aviceda leuphotes burmana* (W. L. Sclater)

(Pl. 7, figs. 3, 6 ; Text-figs. 52, 76, 90)

Degeeriella elbeli Clay, 1958. *Proc. R. ent. Soc. Lond.* (B) **27** : 6, Pl. 1, figs. 3, 6 ; Text-figs. 3, 9, 14, 17. Host : *Aviceda leuphates burmana* (W. L. Sclater).

This species is distinguished from the rest of the species group by the presence of pleural setae on segment V, by the shape of the head and the male genitalia. It is separated from members of the *fulva* group, which it resembles in many characters, by the greater development of the ventral carinae anteriorly, and by a combination



FIGS. 109–122. 109–111.—Central anterior margin of head. 109. *D. fulva* from *Buteo lagopus*. 110. *D. n. nisus*. 111. *D. rufa*. 112–122.—Thoracic sternal plates. 112–118.—*D. fulva* (♂♂) to show variation. 112–114. From *Aquila chrysaëtos*. 115–116. From *Aquila wahlbergi*. 117. From *Buteo lagopus*. 118. From *Buteo buteo*. 119. *D. d. discocephalus* (♂). 120. *D. rufa* (♀) from *F. tinnunculus*. 121. *D. r. regalis* (♀) from *Milvus milvus*. 122. *D. punctifer*. *v*.—ventral preantennal suture.

of the characters of the ventral suture, the marginal carinae of the temples, the pleural thickening of the abdomen and the details of the male genitalia.

MALE. Inner dorsal edge of marginal carina indented medially; ventral suture reaches to or nearly to anterior margin; marginal temporal carinae broad. Tergites II and III show all stages from a slight median concavity to a well marked slit. Pleural thickening with dorsal outline narrow and straight and ventral outline broader and more rounded. Male genitalia as in Pl. 7, fig. 6 and in Text-fig. 52. Internal genitalia are similar to those of *D. fulva* from *Buteo buteo* but the vesicular apparatus is longer (1 specimen: 0·78 mm.) and the lateral lobes are relatively shorter (0·32 mm.).

FEMALE. Terga of IX–XI as in *fulva* Genital region with rather narrower inner genital and subvulval sclerites than in *fulva* (Text-figs. 76, 90).

CHAETOTAXY OF ABDOMEN. Tergocentral setae: II, 4; III–VII normally 6, range 5–8; VIII varies from 3–7; X in the male with one each side, in female with 2 each side. Pleural and sternocentral setae as in *fulva*. Total number of marginal setae of last segment of male varies from 8–10. One female has only 4 tergocentral setae on each of segments III–V.

NYMPHS. Second and third stage nymphs have the anterior margin of the head pointed.

MATERIAL EXAMINED. Holotype male and allotype female and 16 ♂, 13 ♀ paratypes from *Aviceda leuphotes burmana* from Dansai District, Thailand. A small number of specimens from *Aviceda cuculoides* Swainson from Africa differ from the above, but are not in sufficiently good condition for identification.

Measurements in mm.

	Length		Breadth	
	Range	Mean	Range	Mean
Male				
Head (17)	0·55–0·58	0·57	0·43–0·47	0·450
Prothorax (10)	—	—	0·30–0·32	0·315
Pterothorax (10)	—	—	0·48–0·52	0·505
Abdomen (10)	1·20–1·29	1·25	0·58–0·63	0·620
Total (10)	2·12–2·22	2·18	—	—
C.I. (17)	0·78–0·80	0·79	—	—
Genitalia (3)	0·40–0·42	—	—	—
Female				
Head (10)	0·59–0·62	0·61	0·47–0·50	0·48
C.I. (10)	0·78–0·81	0·80	—	—

Degeeriella tendeiroi sp. n.

Type host: *Gampsonyx swainsonii swainsonii* Vigors

(Pl. 6, fig. 2; Text-figs. 37, 53, 92)

This species in general appearance resembles *elani*, but the head is more pointed, the median point being formed by the marginal carina and not in part by the hyaline margin as in *elani*. It is distinguished from other species in the species group, except *elbeli*, by the absence of tergal plates on segments XI of the male and from *elbeli* by the shape of the head.

MALE. Marginal carina pointed medially and inner margin indented; ventral suture does not reach to anterior margin. Tergite II only with median indentation. Pleural thickening broad with inner ventral margin rounded. Genitalia of *fulva* type.

FEMALE. Terga of IX–XI as in *fulva*. Inner genital sclerites as in *elbeli*; subvulval sclerites as in Text-fig. 92.

CHAETOTAXY OF ABDOMEN. Tergocentral setae: II normally 4, range 3–4; III–VI normally 6, range 5–6 (one ♂ with only 3 setae on III); VII–VIII, range 4–6; X in male 2–3 each side, in the female 2 each side. Pleural setae: II–V, 0; remainder as in *fulva*. Sternocentral setae: II, range 2–4, remainder as in *fulva*. Total number of marginal setae of last segment of male varies from 11–12.

MATERIAL EXAMINED. Four ♂, 3 ♀ from *Gampsonyx s. swainsoni* Vigors (skin) from Argentine.

Holotype ♂, *allotype* ♀ in the British Museum (Natural History), slide no. 622 and 3 ♂, 2 ♀ *paratypes* all from *Gampsonyx s. swainsoni* with data as given above.

Named in honour of Dr. João Tendiero in acknowledgment for his co-operation during this study of *Degeeriella*.

Measurements in mm.

Male

	Length Range	Breadth Range
Head (4)	0·48–0·52	0·37–0·38
Prothorax (3)	—	0·25–0·27
Pterothorax (3)	—	0·37–0·43
Abdomen (3)	1·07–1·13	0·48–0·52
Total (3)	1·81–1·93	—
Genitalia (1)	0·28	—
C.I. (4)	0·73–0·77	—

Female

Head (3)	0·48–0·55	0·38–0·41
C.I. (3)	0·74–0·79	—

Degeeriella elani Tendeiro

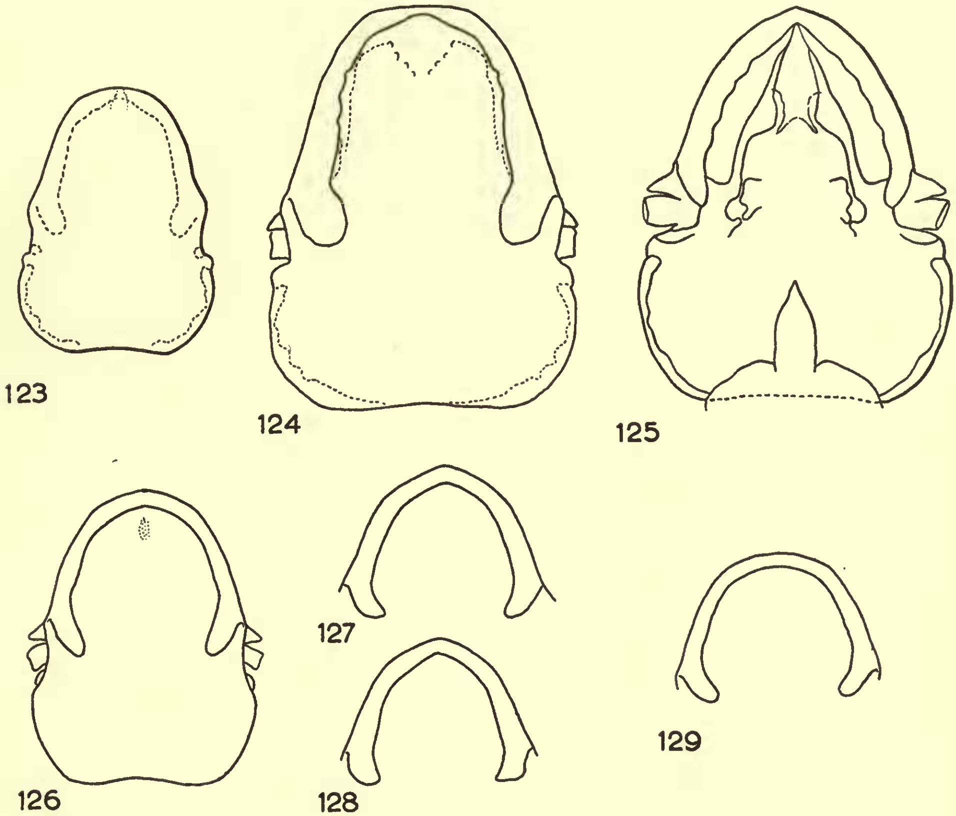
Type host: *Elanus caeruleus* (Desfontaines)

(Pl. 6, fig. 1; Text-figs. 4, 36, 54, 91)

Degeeriella elani Tendeiro, 1955. *Bol. Cult. da Guiné Port.* 9 (35): 598, figs. 36–37, photo. 17–18. Host: *Elanus caeruleus* (Desfontaines).

This species is separated from *elbeli*, *meinertzhageni* and *guimarãesi* by the shape of the head and other characters as given above under the species group; its differences from *tendeiroi* are given above under that species.

MALE. Head pointed anteriorly, the median point is formed largely by the pointed hyaline margin and if this is shrunk or otherwise distorted in a specimen the head will appear less pointed ; inner dorsal margin of marginal carina indented medially ; ventral suture does not reach anterior margin. Tergite II only with median indentation ; tergites of XI present as a small strip of sclerotization each side, immediately



FIGS. 123–129. Heads of *Degeeriella* ; scales various, see measurements. 123. *D. rima* (♂). 124. *D. n. epustulata*, female paratype. 125. *D. meinertzhageni* (♂). 126–128.—*D. rufa carruthi* (♂♂) drawn to same scale to show variation in shape of anterior margin. 129. Preantennal region of *D. rufa.* from *Falco mexicanus*, male paratype.

below suture between segments X and XI. Pleural thickening similar to that of *tendeiroi*. Genitalia as shown in Text-figs. 36, 54 ; there is considerable variation in the height of the ventral endomeral arms. Internal genitalia from a specimen from *Elanus caeruleus vociferus* from Thailand are rather similar to those of *D. fulva* from *Buteo buteo* (Text-fig. 4).

FEMALE. Terga IX–XI with unsclerotized areas round setae usually as in Text-fig. 105, but there is some variation in this character. Genital region as in Text-fig. 91.

CHAETOTAXY OF ABDOMEN. Tergocentral setae: II normally 4, range 4–5; III–V normally 6, range 5–7; VI normally 6, range 4–6; VII normally 4 range 4–6; VIII normally 4, range 4–5; X in the male 1–2 each side, in the female 2 each side. Pleural setae: II–V, 0; rest of pleural setae and sternocentral setae as in *fulva*. Total number of marginal setae, dorsal and ventral of last segment of male varies from 11–14.

MATERIAL EXAMINED. One ♀ paratype from *Elanus caeruleus* without locality; 11 ♂, 17 ♀ from *Elanus c. caeruleus* (Desfontaines) from Kenya, Uganda, N. Rhodesia and the Cameroons; 5 ♂, 4 ♀ from *Elanus caeruleus vociferus* (Latham) from Deccan, India and Thailand; 3 ♂, 1 ♀ from *Elanus notatus* Gould from Cairns, Australia; 3 ♂, 1 ♀ from *Elanus l. leucurus* (Vieillot) from S. Paulo, Brazil.

Measurements in mm.

Male

(10)

	Length		Breadth	
	Range	Mean	Range	Mean
Head	0·47–0·52	0·49	0·36–0·40	0·37
Prothorax	—	—	0·25–0·27	0·26
Pterothorax	—	—	0·35–0·42	0·39
Abdomen	0·96–1·08	1·03	0·45–0·53	0·48
Total	1·71–1·88	1·78	1·71–1·88	1·79
Genitalia (1)	0·35	—	—	—
C.I.	0·73–0·79	0·75	—	—

Female

(10)

	Length		Breadth	
	Range	Mean	Range	Mean
Head	0·50–0·53	0·52	0·38–0·41	0·39
Prothorax	—	—	0·23–0·28	0·27
Pterothorax	—	—	0·42–0·45	0·43
Abdomen	1·23–1·35	1·28	0·55–0·60	0·57
Total	2·02–2·22	2·10	—	—
C.I.	0·73–0·79	0·76	—	—

Degeeriella meinertzhageni Clay, 1958

Type host: *Chelictinia riocourii* (Vieillot)

(Pl. 7, figs. 2, 5; Text-figs. 60, 61, 73, 93, 125)

Degeeriella meinertzhageni Clay, 1958. *Proc. R. ent. Soc. Lond.* (B) **27**: 4, Pl. I, figs. 2, 5; text-figs. 2, 7, 8, 11, 13, 16. Host: *Chelictinia riocourii* (Vieillot).

This species resembles *guimarãesi* most nearly in the form of the ventral carinae and is distinguished by the shape of the head and the male genitalia.

MALE. Inner dorsal margin of marginal carina indented medially; ventral suture does not reach to anterior margin of head; ventral carinae each with flattened edge parallel to that of opposite carina to which is attached a lobe of the pulvinus.

Tergite II only with median indentation ; sclerotization of tergum XI in the form of two small plates variable in size and shape. Genitalia of distinct type as shown in Pl. 7, fig. 5 and Text-figs. 60–61 ; there is some variation in the size of the penial arms and in the position of the setae on the ventral endomeral arms.

FEMALE. Tergites IX–XI with unsclerotized areas as in Text-fig. 107. Genital region as shown in Text-figs. 73, 93 ; inner genital sclerites fused in mid-line.

CHAETOTAXY OF ABDOMEN. Tergocentral setae : II normally 4, range 3–4 ; III–VII normally 6, range 3–8 ; VIII normally 4, range 4–5 ; X in male has 1–2 each side and in the female 2 each side. Pleural setae : II–V, 0 ; VI-VII, one each side, VIII, 3 ; in the male IX has 2 each side and X, 0 ; in the female IX and X each have 1–2 each side. Sternocentral setae : II–VI, 4. In the male total number of marginal setae of last segment varies from 17–24.

NYMPHS. Third instar nymphs have the front of the head pointed as in the adult but the sides of the preantennal region are straighter.

MATERIAL EXAMINED. Holotype male and allotype female and 15 ♂, 9 ♀ paratypes of *D. meinertzhageni* from *Chelictinia riocourii* (Vieillot) from Abyssinia and the Sudan.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (16)	0·50–0·56	0·52	0·38–0·44 (16)	0·40
Prothorax (10)	—	—	0·28–0·31	0·28
Pterothorax (10)	—	—	0·44–0·50	0·47
Abdomen (10)	1·13–1·30	1·22	0·57–0·68	0·63
Total (10)	2·00–2·21	2·08	—	—
Genitalia (3)	0·48–0·50	—	—	—
C.I. (16)	0·73–0·82	0·77	—	—

Female

	Length		Breadth	
	Range	Mean	Range	Mean
Head (10)	0·52–0·57	0·55	0·40–0·45	0·42
Prothorax (5)	—	—	0·28–0·32	0·30
Pterothorax (5)	—	—	0·46–0·52	0·49
Abdomen (5)	1·37–1·44	1·41	—	—
Total (5)	2·33–2·37	2·32	—	—
C.I. (10)	0·73–0·80	0·77	—	—

Degeeriella guimaraesi Clay, 1958

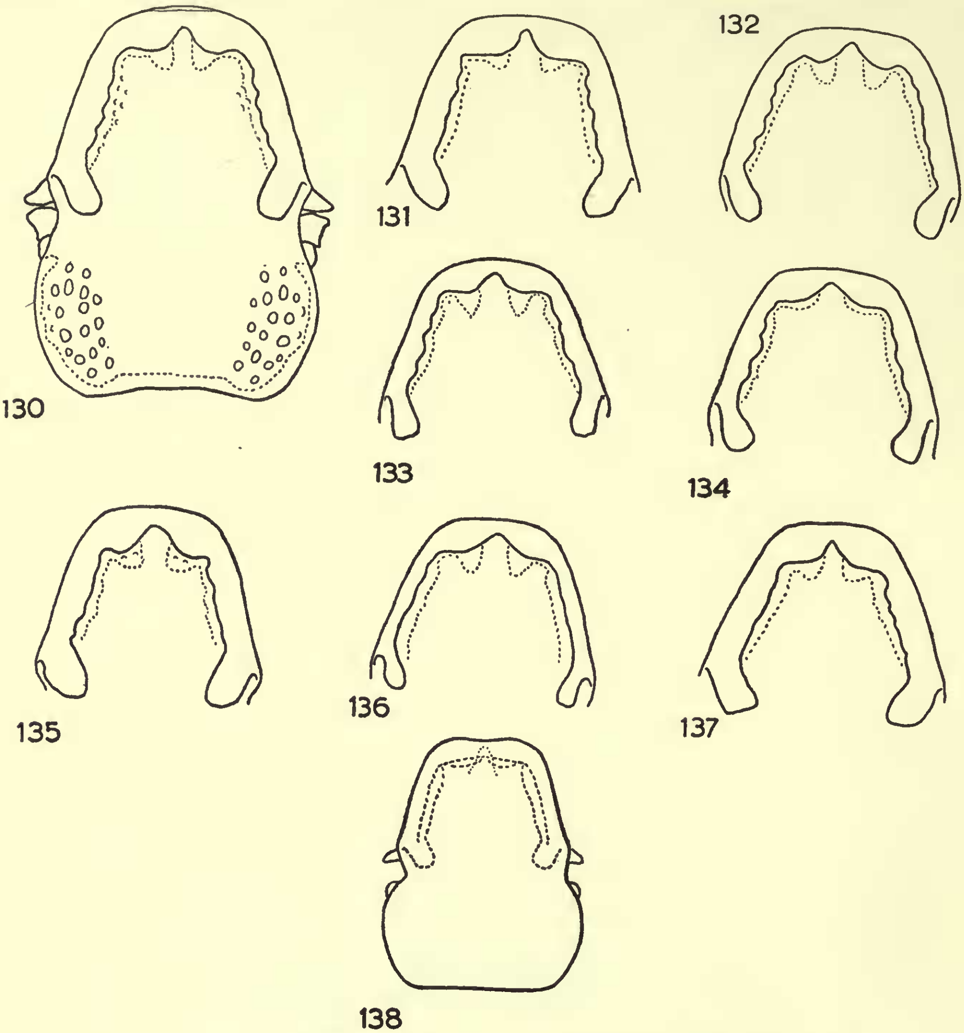
Type host : *Elanoides forficatus forficatus* (Linn.)

(Pl. 7, figs. 1, 4 ; Text-figs. 58, 59, 74, 94, 100)

Degeeriella guimarãesi Clay, 1958. *Proc. R. ent. Soc. Lond.* (B) **27** : 2, pl. I, figs. 1, 4 ; text-figs. 1, 4, 5, 6, 10, 12, 15. Host : *Elanoides f. forficatus* (Linn.).

This is the most distinctive species of the species group, distinguished from all by the characters of the male genitalia and the female genital plate.

MALE. Marginal carina reduced centrally with hyaline margin in this area; inner dorsal margin of marginal carina indented medially; ventral suture does not reach anterior margin; ventral carinae and pulvinus as in *meinertzhageni*; dorsal



FIGS. 130–138. Heads of *Degeeriella*, males. 130–137.—*D. r. regalis* (drawn to same scale) from various hosts to show variation in outline of head and marginal carina. 130–132.—From *Milvus milvus*. 133–134.—From *Buteo swainsoni*. 135–137.—From *Buteo galapagoensis*. 138. *D. regalis* subsp. (♂) from *Gypohierax*.

preantennal region with sculpturing. Tergites II–III without median indentation, but II usually shows a more lightly sclerotized central concave area; shape of fused terga IX–X characteristic (Text-fig. 100); tergal thickening of XI present as a single plate which may be interrupted medially. Pleural thickening narrow.

Genitalia distinctive (Pl. 7, fig. 4; Text-figs. 58–59); penial sclerite present but not joined to penis, setae usually associated with penial arms absent; there is some individual variation in the length of these arms and the dorsal endomeral arms may or may not join parameres.

FEMALE. Tergites IX–XI as in *fulva*. Genital region as shown in Text-figs. 74, 94; genital plate with median prolongation; inner genital sclerites fused in mid-line and inner edge of vulva toothed.

CHAETOTAXY OF ABDOMEN. Tergocentral setae of male: 4; III–IV normally 4, range 4–5; V–VI range 4–6; VII–VIII normally 6, range 4–6; X normally 2 + 2, one specimen with 4 + 4. In the female tergocentral setae fewer in number: II–VIII normally 4, range 3–5; X, 2 + 2. Pleural setae: II–V, 0 (two females have one on each side of V); VI–VII, 2 each side; VIII, 3; in the male IX has 2 and X, 0; in the female IX–X, 1–2 each side. Sternocentral setae: II, 2; III–VI normally 4, range 3–4. Total number of marginal setae dorsal and ventral, of the last segment in the male varies from 10–14.

MATERIAL EXAMINED. Holotype male and allotype female and 9 ♀, 15 ♀ paratypes from *Elanoides f. forficatus* (Linn.) from Florida and from *Elanoides f. yetapa* (Vieillot) from Brazil.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (9)	0·57–0·58	0·575	0·43–0·46	0·44
Prothorax (6)	—	—	0·32–0·35	0·33
Pterothorax (6)	—	—	0·47–0·50	0·49
Abdomen (6)	1·12–1·18	1·15	0·55–0·65	0·60
Total (6)	2·00–2·15	2·08	—	—
Genitalia (2)	0·42–0·44	—	—	—
C.I. (9)	0·74–0·79	0·76	—	—

Female

	Length Range	Length Mean	Breadth Range	Breadth Mean
Head (10)	0·58–0·62	0·60	0·45–0·48	0·47
Prothorax (10)	—	—	0·33–0·37	0·35
Pterothorax (10)	—	—	0·49–0·55	0·52
Abdomen (8)	1·17–1·38	1·30	—	—
Total (8)	2·20–2·33	2·27	—	—
C.I. (10)	0·75–0·79	0·77	—	—

The rufa *Species Group*

1–3. As in *fulva* group.

4. Outline of thoracic sternal plate rather more rounded than in *fulva* group, and as in this group shows individual variation in shape, and arrangement and number of setae.

5. As in *fulva* group.

6. Tergal plates of segment XI apparent in male.

7. Terga of segments IX–XI of female as in Text-fig. 107.
8–10. As in *fulva* group.
11. Female genital plate with median posterior prolongation.
12. As in *fulva* group.
13. As in Pl. 8, fig. 7, penial sclerite absent.
14. As in *fulva* group.
15. Pleural setae absent on II–III and present on X of male.
16. Sternocentral setae of segments III–VI average more than 5 per segment.
17. As in *fulva* group.

This species group contains a single species which has a superficial resemblance to members of the *fulva* group, but is, however, quite distinct from these and other species considered here in having 2 pleural setae each side of segment X in the male and in the absence of the penial sclerite ; in the female it differs from all other species, except *D. guimarãesi*, in the form of the genital plate. The ventral carinae and pulvinus of the nymph resemble those of the nymphs and adults of this latter species.

Degeeriella rufa rufa (Burmeister), 1838

Type host : *Falco tinnunculus* Linn.

(Pl. 6, fig. 3 ; Pl. 8, fig. 7 ; Text-figs. 5, 10, 18–22, 38, 55, 75, 95, 104, 107, 111, 120, 129, 139–164)

Nirmus rufus Burmeister, 1838. *Handb. Ent.* **2** : 430. Host : *Falco tinnunculus* Linn.

Nirmus rufus was described by Burmeister from specimens in the Nitzsch collection from which the figure in Giebel, 1874 (pl. 7, figs. 11–12) were made ; these figures represent the species described below.

The characters distinguishing *D. rufa* are given above under the definition of the species group of which it is the only species.

Male. Inner edge of marginal carina not or slightly indented medially ; ventral suture variable in form, does not reach anterior margin of head (Text-fig. 111). Tergites II–III with median indentation, that of III occasionally being partly occluded ; tergites of XI present as two well marked sclerites. Pleurites as in Text-fig. 104. Genitalia as in Pl. 8, fig. 7, and Text-figs. 38, 55 ; penial sclerite absent. Internal genitalia characteristic (Text-fig. 5).

Female. Fused terga of IX–XI with a continuous unsclerotized area round the two setae each side (Text-fig. 107). Genital region as in Text-figs. 75, 95 ; genital plate differs from all other known species except *guimarãesi* in having a central posterior prolongation (Text-fig. 95).

Chaetotaxy of abdomen. Tergocentral setae : II, normally 6, range 5–8 ; III–VI, normally 8, range 6–11 ; VII normally 6, range 5–8 ; VIII range 4–8, in the female rarely less than 6 ; X, 2 each side. Pleural setae : II–III, 0 ; IV–V, 1 each side ; VI–VII, 2 ; VIII, 3 ; IX–X, 2 each side. Sternocentral setae : II, normally 5, range 4–6 ; III–VI normally 6, range 5–7. Total number of marginal setae of last segment of male varies from 10–14.

NYMPHS. All nymphal instars of this species are available and have been discussed above, p. 129 and figured (Text-figs. 10, 18–22).

Measurements in mm.

D. rufa *from* Falco t. tinnunculus

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (57)	0·46–0·55	0·50	0·37–0·44	0·40
Prothorax (20)*	—	—	0·25–0·29	0·26
Pterothorax (20)	—	—	0·33–0·42	0·37
Abdomen (50)	1·05–1·32	1·15	0·48–0·67 (20)	0·53
Total (20)	1·78–2·03	1·90	—	—
Genitalia (10)	0·41–0·44	0·43	—	—
Head index (56)	0·75–0·83	0·795	—	—
Head index A (28)	0·80–0·86	0·83	—	—

* First 20 picked at random. A. Head index of specimens from *F. rusticolus islandus*.

Female

(20)

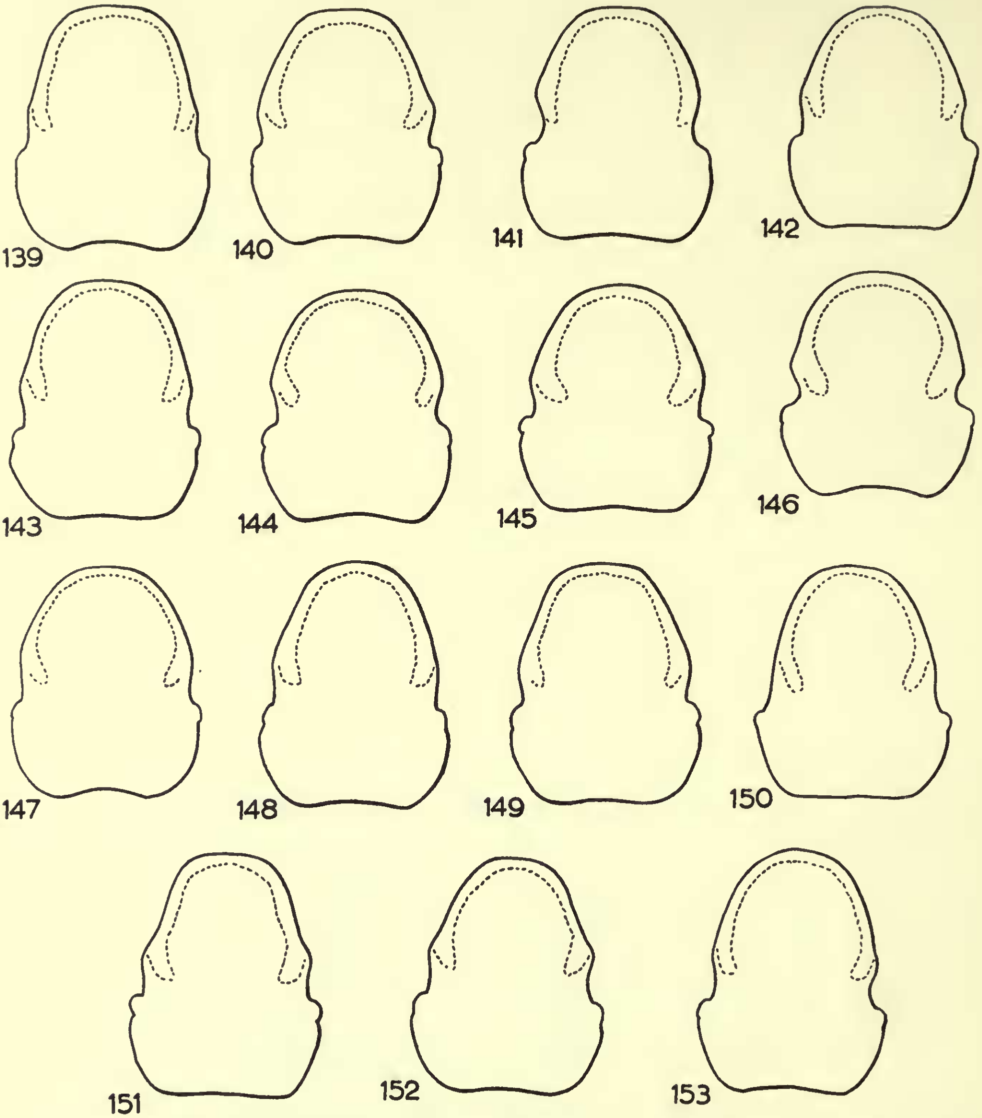
Head	0·50–0·57	0·53	0·40–0·45	0·43
Prothorax	—	—	0·26–0·29	0·28
Pterothorax	—	—	0·37–0·43	0·41
Abdomen	1·23–1·40	1·31	0·53–0·63	0·59
Total	2·01–2·25	2·14	—	—
Head index	0·78–0·83	0·80	—	—

TABLE I.—*Average Number of Total Tergocentral Setae of Abdominal Segments II-VIII and Breadth of Head at Temples in Males of* D. rufa *from Various Species of* Falco

	Tergocentral setae	Breadth of head in mm. Range	Mean
A	47·6 (30)	0·33–0·40 (51)	0·37
B	—	0·37–0·43 (14)	0·39
C	49·5 (14)	0·38–0·41 (18)	0·40
D	50·6 (51)	0·37–0·44 (57)	0·40
E	52·3 (40)	0·38–0·44 (42)	0·41
F	—	0·40–0·42 (8)	0·41
G	51·9 (11)	0·40–0·43 (9)	0·42
H	51·2 (22)	0·41–0·43 (7)	0·42
I	53·1 (18)	0·40–0·45 (28)	0·43

A, *F. sparverius*; B, *F. subbuteo*; C, *F. columbarius*; D, *F. tinnunculus*; E, *F. jugger*; F, *F. vespertinus*; G, *F. peregrinus*; H, *F. biarmicus*; I, *F. rusticolus*; number of specimens given in brackets.

VARIATION AND HOST DISTRIBUTION. Over 1,160 specimens have been examined from 19 of the 38 species of *Falco*. With the exception of the population from *Falco sparverius* no differences could be found between the populations from the various hosts except in measurements, number of abdominal setae and characters



FIGS. 139–153. Heads of *D. rufa* from various species of *Falco*. Scale adjusted so that breadth of temples is approximately the same in all figures, actual breadth of head is given after host name. 139. *Falco biarmicus* subsp. 140. *F. b. biarmicus*, 0·42 mm. 141. *F. c. cherrug*, 0·45 mm. 142. *F. jugger*, 0·42 mm. 143–145.—*F. rusticolus islandus*. 143. 0·42 mm. 144. Paratype of *D. fasciata* (Rudow), 0·43 mm. 145. 0·45 mm. 146–147.—*F. rusticolus candicans*. 146. 0·43 mm. 147. 0·41 mm. 148–149.—*F. peregrinus calidus*. 148. 0·40 mm. 149. 0·41 mm. 150. *F. s. subbuteo*, 0·38 mm. 151–153.—*F. eleonorae*. 151. 0·42 mm. 152. 0·38 mm. 153. 0·39 mm.

of the preantennal region of the head. In the case of the measurements of the head breadth some populations averaged larger but there was overlap between individuals of most of the populations measured (Table I). Again some populations averaged a larger number of tergocentral setae but there were individuals in all populations with a similar number of setae on each segment. A statistical analysis of these numbers may show that the differences between some of these populations are significant, but it is not considered that such populations should be recognized taxonomically on these characters alone. As pointed out by Tendeiro (in press) there is in addition marked differences in the shape of the preantennal region of the head in the populations from some of the species of *Falco* making them easily recognizable, while between others the differences are slight. These differences are also reflected in the nymphs, which in some cases (Text-figs. 21–22) differ more in this stage than in the adults (Text-figs. 144, 147). The problem is further complicated by some populations showing considerable individual variation; three specimens (Text-figs. 151–153) from *Falco eleonorae* taken from the same host and subjected to the same treatment might be included in three different subspecies; the specimen from *F. biarmicus* (Text-fig. 139) is more similar to that from *F. peregrinus* (Text-fig. 149) than are the specimens from these two hosts shown in Text-figs. 140, 148. Variation in specimens from other hosts are shown in Text-figs. 143–145, 146–147 and 163–164. Further, it is not possible to reduce these differences to mathematical terms and the human eye is easily subject to optical illusions.

There is a tendency in some cases for the populations in which the members average larger for these to have the preantennal region of the head more rounded (cf. Text-figs. 146 and 150, 142 and 155) and to average a greater number of abdominal setae; the increase in size of the specimens is roughly related to the size of the host. Thus, similar-sized species of *Falco* may be parasitized by *Degeeriella* with similar average size, a similar number of abdominal setae and heads of a rather similar shape even though these falcons may not be closely related. If the subgeneric divisions of *Falco* as given in Peters (1931) are taken as a measure of relationship, then the not closely related *F. peregrinus* and *F. biarmicus* of similar size are found to have parasites with similar average measurements for the breadth of the head, average number of abdominal setae and a rather similar shaped head (Text-figs. 139, 149) whereas those from the related *tinnunculus* and *sparverius* differ on the larger host by having a larger average measurement of the head with a less narrowed anterior margin and a larger number of abdominal setae. Thus, two or three differences between two populations may all be associated with difference in size which is itself correlated with differences in host size and does not, therefore, necessarily reflect relationship. This is shown in Table I which gives the head measurements and tergocentral setae; these are arranged in order of increasing size of the breadth of the head. It will be seen that this reflects the size of the hosts, but an exact numerical comparison is not possible as the races of different species of hawks overlap, thus the larger races of the "smaller" *Falco* may overlap with the smaller races of the "larger" species, and moreover the males of the smaller races of the "larger" species may be smaller than the females of the "smaller" species. More material is required from some species to confirm that the differences between the *Degeeriella* populations are significant and adequate samples of parasites from the different races of a species such as *F. peregrinus*, which vary considerably in size, must be measured to see whether those from the smaller races differ from those from the larger. In addition, there is some similarity between the shape of the heads of specimen from related hosts, e.g. those from *F. rusticolus* and *F. jugger*. Thus, the size and shape of the head may reflect either relationship or size of the host irrespective of relationship. Figs. 139–164 show the outline of the anterior margin of the heads of specimens from various species of *Falco* and the related *Ieracidea* ; these are not drawn to the same scale but in such a way that the breadth of the temples is the same throughout, this enables a more accurate comparison of shape to be made. It will be seen from these figures that while some of the populations are quite distinct, others, especially taking into account individual variation, are doubtfully separable. As already discussed above it must be largely a matter of personal opinion as to which of these populations should be recognized taxonomically and it is possible that the systematics might be simplified by considering them as belonging to a single species with a tendency to develop local populations on the different species of *Falco*. The recognition by name of the more distinct populations must result in the endless proliferation of names for those which vary slightly in size, proportions and curvature of the anterior margin, often depending on the individual specimen available. Names have been given to many of the populations, as listed below, and the present writer does not at the moment intend to increase these by naming other populations which do not exactly correspond to these ; this should perhaps wait until adequate series have been seen from more species of *Falco* and their races.

Names Given to the Different Populations of D. rufa *from* Falco

Nirmus fasciatus Rudow, 1869. *Beitr. Kennt. Malloph.* : 20. Host : *Falco islandicus* = *Falco rusticolus islandus* Brunnich.

Nirmus quadraticollis Rudow, 1870. *Z. ges. NatWiss.* **35** : 469. Host : *Falco vespertinus* Linn.

Nirmus nitzschi Giebel, 1874. *Insecta epizoa* : 125, *nec N. nitzschi* Ponton, 1871. Host : *Falco subbuteo* Linn., *F. aesalon* = *F. columbarius aesalon* Tunstall and *F. peregrinus* Tunstall. See *D. drosti.*

Nirmus burmeisteri (Giebel), 1874. *Insecta epizoa* : 126. Host : *Falco rufipes* = *Falco vespertinus* Linn.

Nirmus platyclypeatus Piaget, 1880. *Pediculines* : 145, pl. 12, fig. 1. Host : *Motacilla alba.* Error = *Falco* sp.

Kélerinirmus rufus boliviensis Eichler, 1954. *Beitr. Fn. Perus*, **4** : 38. Host : *Falco fuscocaerulescens pichinchae* Chapman.

Degeeriella rufa drosti Timmermann, 1955. *Náttúrurufraedingurinn*, **1** : 49. *Nomen novum* for *Nirmus nitzschi* Giebel *nec* Ponton, 1871. Host restriction to *Falco columbarius.*

Degeeriella falconoides Carriker, 1956. *Florida Ent.* **39** : 42, figs. Host : *Falco mexicanus* Schlegel.

[1] *Degeeriella masumae* Ansari, 1955. *Proceedings VIIth Pakistan Sci. Conf.*, Biology : 42. Host : *Falco jugger* Gray.

[1] *Degeeriella splendidus* Ansari 1955. *Proceedings VIIth Pakistan Sci. Conf.*, Biology : 42. Host : *Cerchneis tinnunculus interstinctus* McClell = *Falco tinnunculus interstinctus* Horsfield.

[1] The interpretation of these names is doubtful, see below, p. 199.

MATERIAL EXAMINED. ♂ lectotype and 2 ♂, 3 ♀ paratypes of *Nirmus fasciatus* Rudow (see Clay & Hopkins, 1955 : 59) ; ♂ lectotype and 5 ♂, 3 ♀ paratypes of *Nirmus quadraticollis* Rudow (see Clay & Hopkins, 1955 : 59) ; ♂ lectotype (slide no. 1388), Piaget collection in the British Museum (Nat. Hist.) and 1 ♂, 1 ♀ paratypes of *Nirmus platyclypeatus* Piaget ; 1 ♂, 1 ♀ paratypes of *Degeeriella falconoides* Carriker ; 4 ♂, 4 ♀ paratypes of *D. rufa applanata* Tendeiro. Over 1,000 specimens (males and females) from the following species of *Falco* : *F. biarmicus* Temminck from Sinai, Somaliland, Tanganyika, Natal and Cape Colony ; *F. cherrug* J. E. Gray from Czechoslovakia and India ; *F. mexicanus* Schlegel from U.S.A. and Mexico ; *F. jugger* J. E. Gray from Afghanistan and India ; *F. rusticolus* Linn. from Greenland, Iceland, Norway and Canada ; *F. peregrinus* Tunstall from Czechoslovakia, Egypt, Sudan, Ceylon, Mandalay and British Columbia ; *F. subbuteo* Linn. from Finland, Uganda, Tanganyika, and Afghanistan ; *F. cuvierii* A. Smith from French Cameroons; *F. eleonorae* Géné from Morocco, Crete and Cyprus ; *F. concolor* Temminck from Egypt ; *F. hypoleucos* Gould from New South Wales, Australia ; *F. fuscocaerulescens* Vieillot from S. Paulo, Brazil ; *F. columbarius* Linn. from British Isles and Hungary ; *F. ardosiaceus* Vieillot from Portugese Guinea and Uganda ; *F. vespertinus* Linn. from Fair Isle, Estonia and Cyprus ; *F. amurensis* Radde from Kenya ; *F. naumanni* Fleischer from Palestine, Kenya and Afghanistan ; *F. tinnunculus* Linn. from British Isles, France, Switzerland, Poland, Madeira, Asia Minor, Palestine, Jordan, Egypt, Uganda, Tanganyika, Cape Colony, Aden, Northern India, Ladak, Sikkim, Manipur and Burma ; *Falco alopex* (Heuglin) from the Sudan. Eleven ♂, 22 ♀ from *Ieracidea orientalis* (Schlegel), no data.

Degeeriella rufa carruthi Emerson, 1953

Type host : *Falco s. sparverius* Linn.

(Text-figs. 126–128)

Degeeriella carruthi Emerson, 1953. *J. Kansas ent. Soc.* **26** : 132, pl. 1, figs. 2, 5. Host : *Falco s. sparverius* Linn.

This subspecies differs from the nominate form in the narrower preantennal region, the anterior margin sometimes being rather pointed, but this pointed appearance is absent in some specimens (cf. Text-figs. 126–128). In addition, both sexes can be recognized by the sculpturing of the middle of the dorsal surface of the head near the anterior margin, this appears as a small dark mark in fresh specimens ; this is sometimes also apparent to a lesser extent in specimens of *D. r. rufa*. In the male there is only one seta each side of the ventral endomeral arm instead of the usual two. Second and third stage nymphs resemble those of *r. rufa* in the shape of the head. Breadth of the head in the male : range 0·33–0·40 mm., mean 0·37 (51 specimens) and in the female : range 0·37–0·46 mm., mean 0·41 (85 specimens).

MATERIAL EXAMINED. One ♂, 1 ♀ paratypes of *D. carruthi* Emerson ; 81 ♂, 90 ♀ from subspecies of *F. sparverius* Linn. from Alaska, British Columbia, various localities in the United States of America, Cuba, British West Indies and Brazil.

The regalis *Species Group*

1–11. As in *fulva* group.
12. Female inner genital sclerites may or may not be fused in mid-line.
13. Male genitalia of unique type (Text-fig. 56); penial sclerite present.
14. As in *fulva* group.
15. Pleural setae absent on II–III.
16. Sternocentral setae of segments III–VI normally 6–8.
17. As in *fulva* group.

This species group which has a superficial resemblance to the *fulva* group can be distinguished in both sexes by the greater number of sternocentral setae and in the males by the genitalia.

Degeeriella regalis regalis (Giebel), 1886

Type host: *Milvus m. milvus* (Linn.)

(Pl. 5, fig. 1; Text-figs. 6, 39, 56, 80, 81, 121, 130–137)

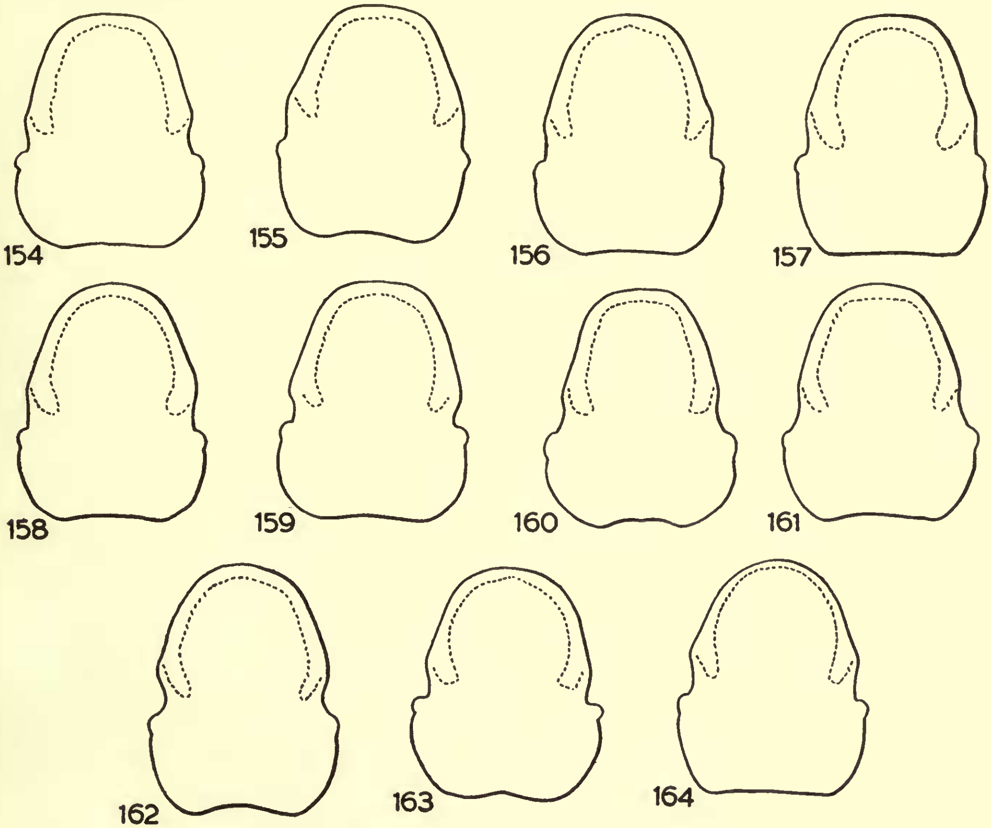
Nirmus regalis Giebel, 1866. *Z. ges. NatWiss.* 28 : 364. Host: *Milvus regalis* = *Milvus m. milvus* (Linn.).
Nirmus vittatus Giebel, 1874. *Insecta epizoa*: 127. Host: *Milvus ater* = *Milvus migrans migrans* (Boddaert).
Nirmus appendiculatus Piaget, 1880. *Pédiculines*: 132, pl. 11, fig. 2. Host: *Milvus ater* = *Milvus migrans migrans* (Boddaert) and *Milvus migrans aegyptius* (Gmelin).
Nirmus incertus Piaget, 1885. *Pédiculines Supplément*: 20, pl. 2, fig. 9. Host: *Totanus glottis*. [Error. Probably *Milvus* sp.]
Nirmus curvilineatus Kellogg & Kuwana, 1902. *Proc. Wash. Acad. Sci.* **4** : 470, pl. 29, fig. 4. Hosts: *Nesopelia galapagoensis* and *Oceanites gracilis*. [Error. Probably *Buteo galapagoensis* (Gould).]
Nirmus pseudophaeus Carriker, 1903. *Univ. Stud. Neb.* **3** : 143, pl. 3, fig. 1. Host: *Pezopetes capitalis*. [Error. Probably *Buteo swainsoni* Bonaparte.]

Nirmus regalis was the name given by Giebel in 1866 to the description of a "*Nirmus* spec. indet." from *Milvus regalis* appearing in Giebel, 1861 (*Z. ges. NatWiss.* **17** : 524).

Male. Head as shown in Pl. 5, fig. 1 with ventral suture as in *fulva*. Tergite II only with median indentation. Pleural thickening as in *fulva* but broader. The genitalia (Text-fig. 56) differ from all other known species of *Degeeriella* in the form of the penis and in the presence of an anteriorly curved sclerite each side. Most specimens have the usual two setae on each ventral arm of the endomeral plate, but some may have one arm with one seta; the dorsal arms are usually fused to the side of the basal apodeme, but may be interrupted on one side. There is variation in the length of the penis and the curvature of the lateral margins of the dorsal endomeral plate. The internal genitalia are of characteristic form (Text-fig. 6).

Female. The genital region differs from all preceding species and from the other subspecies of *regalis* in having the two inner genital sclerites either fused together or closely approximated in the mid-line (Text-figs. 80–81).

CHAETOTAXY OF ABDOMEN. Tergocentral setae: II normally 6, range 5–7; III–VII normally 8, range 7–10; VIII normally 6–7, range 5–8; X in the male



FIGS. 154–164. Heads of *D. rufa* from various species of *Falco* and *Ieracidea* (as figs. 139–153). 154. *Falco cuvierii*, 0·42 mm. 155. *F. concolor*, 0·40 mm. 156. *F. hypoleucos*, 0·39 mm. 157. *F. fuscocaerulescens* subsp. ?, 0·38 mm. 158. *F. columbarius subaesalon*, 0·40 mm. 159. *F. ardosiaceus*, 0·41 mm. 160. *Falco* sp. ? Lectotype of *D. platyclypeata* (Piaget), 0·42 mm. 161. *Falco vespertinus*, 0·38 mm. 162. *F. t. tinnunculus*, 0·39 mm. 163–164.—*Ieracidea orientalis*. 163. 0·42 mm. 164. 0·40 mm.

normally 2 each side, range 1–3, female 2 each side. Pleural setae: II–III, 0; IV–V, 1 each side: VI–VII, 2; VIII, 3; IX in the male normally 2, occasionally 3 each side; X, 0; IX–X in the female 2, occasionally 3 each side. Sternocentral setae: II normally 6, range 4–7, III–VI normally 8, range 6–9; VII in the male varies from 2 to 4 each side; VIII–XI as in *fulva*. Total number of marginal setae, dorsal and ventral, in the male varies from 11–16.

NYMPHS. Second and third instars have been seen from *Milvus migrans parasitus*, except for the normal shorter preantennal region, these resemble the adult in the curvature of the anterior margin of the head.

Specimens from *Buteo galagapoensis* appear to be indistinguishable from those from *Buteo swainsoni*, except that on the available material they average slightly larger in size. It has also not been possible to distinguish these from specimens from *Milvus*, that is *Degeeriella regalis*. The shape of the anterior margin of the head and the thickness of the marginal carina are characters which are found to vary within the populations from the different host species (see Text-figs. 130–137); other characters which vary within the populations are the shape of the gular and thoracic sternal plates, the curvature of the anterior and posterior margins of tergal plate IX–X in the male and the area of junction between the inner genital sclerites; the apparent differences in the length of the penis and shape of the parameres probably depend on the preparation of the specimens. The only character which shows some degree of constancy is the junction of the dorsal endomeral arms with the basal apodeme: in specimens from *Milvus* the arms are usually joined to the basal apodeme each side (34 specimens) and rarely interrupted on one side (5 specimens), whereas in specimens from *Buteo swainsoni* and *B. galapagoensis* the arms are usually separate on both sides (10 specimens) and rarely joined on one side (2 specimens). However, the number of specimens especially from *Buteo*, in which this character can be seen is small and as there is some overlap it does not seem to be desirable to separate the two on this character. Specimens from *Haliaeëtus leucoryphus* show an even distribution between arms joined on one (8 specimens) or neither side (8 specimens) and more rarely specimens (3) with the arms joined on both sides. It is considered, therefore, more satisfactory to include the populations from the two *Buteo* species under *D. r. regalis* and to sink the names *D. curvilineata* and *D. pseudophaea* Carriker as synonyms. The population on *Haliaeëtus vocifer* is however a recognizable subspecies (see below under *D. regalis castanea*).

Specimens from *Haliastur indus* (Boddaert) are found to differ in different localities. Those from Thailand and Ceylon can be separated from *regalis* on a number of characters and are described below as a new subspecies. Specimens from this host collected in Mulug, Deccan (7 ♂, 13 ♀,) Bharatpur, Rajputana (6♂, 4 ♀), Lucknow (1 ♂, 1 ♀) and Dili, Timor (2 ♂, 2 ♀, host not confirmed) cannot be distinguished from *r. regalis*. Collecting records (none from Timor) show that these specimens could not have come from any species of *Milvus*. At present it is not possible to suggest any explanation for this distribution, further species of *Degeeriella* are needed from *Haliastur indus* throughout its range.

Degeeriella regalis has an interesting distribution: it occurs on all the species of *Milvus* (restricted to the Old World), *Buteo galapagoensis* and *Buteo swainsoni* (both restricted to the New World) and possibly *Haliaeetus leucoryphus* (found in eastern Europe and central Asia,) but fresh material is required for certain identification. Specimens have also been found on one individual of *Buteo jamaicensis* in circumstances which preclude contamination after death. Subspecies are found on *Gypohierax angolensis*, *Haliaeëtus vocifer* and on *Haliastur indus* in parts of its range. It seems possible that *regalis* and *fulva* may derive from a common ancestor, that they later became sympatric, both having a wide distribution and that *regalis* has since become extinct on many species, perhaps lingering on rarely on some, as suggested by the specimens found on *Buteo jamaicensis* sympatric with *fulva*: while *fulva* has become extinct on *Milvus*, *Buteo galapagoensis* and *B. swainsoni*.

Degeeriella curvilineata (Kellogg & Kuwana) was described from a male alleged to have come from *Nesopelia galapagoensis* and a female from *Oceanites gracilis* collected by the Hopkins Stanford Galapagos Expedition of 1898–99. The figure of the male shows this to be a typical hawk *Degeeriella*. The only hawk collected by this expedition in the Galapagos (see Snodgrass & Heller, 1904) was *Buteo galapagoensis* (Gould) which must therefore be assumed to be the true host of *D. curvilineata*. Dr. K. C. Emerson has most kindly examined the two syntypes of this species and tells me that these both have more than four setae on the sterna of abdominal segments III–V; this fact together with the original figure show that *curvilineata* must be identical with specimens in the British Museum (Natural History) from *Buteo galapagoensis* and thus becomes a synonym of *r. regalis*.

Degeeriella pseudophaea (Carriker). Through the kindness of Mr. Carriker it has been possible to examine the type of this species. This is a single female which in the characters of the chaetotaxy, form of abdominal terga II–III and in having the subvulval plates fused in the mid-line resembles the species found on *Buteo swainsoni*. The head in size and general shape also resembles that of this species but the marginal carina is markedly different; however, a teneral specimen from this host has a similar form of narrow marginal carina and there seems little doubt that *pseudophaea* is straggler from this host and a synonym of *Degeeriella r. regalis* (Giebel).

MATERIAL EXAMINED. One ♂, 1 ♀ from *Milvus aegyptiacus* and 3 ♀ from *Milvus ater* types of *Nirmus appendiculatus* Piaget; 1 ♀ type of *Nirmus incertus* Piaget from type host; 1 ♀ holotype of *Nirmus pseudophaeus*; 18 ♂, 15 ♀ from *Milvus m. milvus* (Linn.) from Germany, Czechoslovakia, Jugoslavia and the U.S.S.R.; 70 ♂, 96 ♀ from *Milvus migrans migrans* (Boddaert), *M. m. parasitus* (Daudin), *M. m. arabicus* Swan and *M. m. govinda* Sykes from Italy, Greece, Kenya, Uganda, NW. Rhodesia, Bechuanaland, Saudi Arabia, Aden, Deccan, India and Nepal; 4 ♂, 2 ♀ from *Milvus l. lineatus* (J. E. Gray) from Thailand; 9 ♂, 15 ♀ from *Buteo galapagoensis* (Gould) from the Galapagos Islands; 9 ♂, 15 ♀ from *Buteo swainsoni* Bonaparte from North America; 1 ♂, 12 ♀ from *Buteo jamaicensis borealis* (Gmelin) from Arizona; 14 ♂, 19 ♀ from *Haliastur i. indus* (Boddaert) from Deccan, Rajputana and Lucknow in India; 36 ♂, 28 ♀ from *Haliaeetus leucoryphus* (Pallas) from various localities in India.

Neotype of *Nirmus regalis* Giebel: ♂ (slide no. 626) in the British Museum (Natural History) from *Milvus m. milvus* from Czechoslovakia. Neallotype, ♀ and neoparatypes, 17 ♂, 14 ♀ from the same host from Germany, Czechoslovakia, Jugoslavia and U.S.S.R.

Lectotype of *Nirmus appendiculatus*: ♀ (slide no. 1182) in the Piaget collection of the British Museum (Natural History) from *Milvus aegyptiacus*. Paratypes: 1 ♀ from *Milvus aegyptiacus* and 3 ♀ from *Milvus ater*.

Lectotype of *Nirmus incertus*: ♀ (slide no. 740) in the Piaget collection of the British Museum from *Totanus glottis*.

Degeeriella regalis deignani subsp. n.

Type host : *Haliastur i. indus* (Boddaert)

(Pl. 5, fig. 2 ; Text-fig. 40)

This subspecies differs from the nominate form in the average larger size of the head (the specimens from Ceylon average rather smaller than those from Thailand) and in the slightly different shape of the preantennal region. In the male the shape of the tergite on fused IX–X is intermediate between that of *regalis* and *castanea*, the shape of the endomeral plate differs (Text-fig. 40) and segments II–VI have fewer sternal setae (normally 6 per segment) ; in the female the inner genital sclerites are widely separated. This subspecies is distinguished from *r. castanea* by the shape and colour pattern of the head, and the shape of the endomeral plate and tergite of IX–X in the male. A third instar nymph examined has the anterior margin of the head rather more pointed than those of *r. regalis* or *r. castanea*.

MATERIAL EXAMINED. Five ♂, 7 ♀ from *Haliastur i. indus* from Thailand ; 3 ♂, 3 ♀ from Burma and 6 ♂, 4 ♀ from Ceylon.

Holotype male and allotype female, slide no. 619 in the British Museum (Natural History) from *Haliastur i. indus* (Boddaert), no. RE 2490, from Khlong Khlung district, Thailand, collected by R. Elbel and H. G. Deignan, 28th April, 1953. *Paratypes* : 14 ♂, 13 ♀ from the same host form from Thailand, Burma and Ceylon.

Degeeriella regalis castanea (Piaget), 1890

Type host (emended) : *Haliaeëtus vocifer* (Daudin)

(Pl. 5, fig. 3 ; Text-fig. 82)

Nirmus castaneus Piaget, 1890. *Tijdschr. Ent.* **33** : 232, pl. 8, fig. 9. Host : *Sula piscatrix.*

There is a single male in the Piaget collection with this name and host which agrees with Piaget's figure ; it is the same as specimens from *Haliaeëtus vocifer* and preseumably came from that host.

This subspecies can be distinguished from the nominate form in both sexes by the greater amount of sculpturing on the dorsal surface of the preantennal region of the head (not always apparent in treated specimens) and by the colour pattern of the marginal carina. In the male the fused sclerite of terga IX–X is less arched and narrowed medianly, and in the female the inner genital sclerites are widely separated in the mid-line. The number of sternal setae of segments II–VI average less and both sexes average larger in size. Second and third instar nymphs resemble those of *r. regalis* but have the anterior margin of the head somewhat broader and more rounded.

MATERIAL EXAMINED. One ♂ (slide no. 967) in the Piaget collection ; 15 ♂, 27 ♀ in the collections of the British Museum (Natural History), G. H. E. Hopkins and the Natal Museum from *Haliaeëtus vocifer* (Daudin) from Uganda and Natal.

Lectotype of *Nirmus castaneus* Piaget : ♂ (slide no. 967) in the Piaget collection, British Museum (Natural History).

Degeeriella regalis subsp.

Type host : *Gypohierax angolensis* (Gmelin)

(Text-fig. 138)

Tendeiro (in press).

This subspecies resembles most nearly *D. r. castanea* in the form of terga IX–X and number of sternal setae in the male and the form of the inner genital sclerites of the female ; it is distinguished by the shape of the head (Text-fig. 138). On the available material it is not possible to say whether the absence of pigment is secondary due to the method of treatment nor whether the male genitalia differ in any details from those of the nominate form. In the female the inner genital sclerites are not fused or approximated in the mid-line. Tergocentral setae of male holotype : II, 6 ; III–VII, 8 ; VIII, 6. Sternocentral setae : II, 6 ; III–IV, 7 ; V–VI, 6. The tergal setae of the male are somewhat shorter and stouter than in *r. regalis*.

MATERIAL EXAMINED. Two ♂, 1 ♀ from the type host from Piche, Gabu and Mansoa in Portugese Guinea.

Measurements in mm.

D. r. regalis *from* Milvus milvus.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (10)	0·52–0·58	0·55	0·38–0·43 (18)	0·40
Prothorax (10)	—	—	0·26–0·28	0·28
Pterothorax (10)	—	—	0·43–0·49	0·46
Abdomen (10)	1·05–1·23	1·15	0·52–0·63	0·57
Total (10)	1·87–2·17	2·02	—	—
Genitalia (1)	0·40	—	—	—
C.I. (10)	0·74–0·78	0·76	—	—

Female

	Length		Breadth	
	Range	Mean	Range	Mean
Head (10)	0·57–0·60	0·58	0·41–0·46 (12)	0·44
Prothorax (10)	—	—	0·28–0·30	0·29
Pterothorax (10)	—	—	0·49–0·53	0·51
Abdomen (10)	1·37–1·48	1·41	0·60–0·70	0·65
Total (10)	2·25–2·43	2·33	—	—
C.I. (10)	0·74–0·80	0·77	—	—

Degeeriella r. deignani

Male head

	Thailand (5)		Ceylon (5)	
	Range	Mean	Range	Mean
Length	0·57–0·60	0·58	0·57–0·58	0·57
Breadth	0·42–0·45	0·43	0·41–0·43	0·42

Degeeriella r. castanea

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (15)	0·55–0·60	0·57	0·41–0·45	0·43
Prothorax (10)	—	—	0·27–0·32	0·29
Pterothorax (10)	—	—	0·42–0·50	0·47
Abdomen (10)	1·17–1·32	1·24	0·52–0·67	0·59
Total (10)	2·05–2·25	2·14	—	—
Genitalia (3)	0·41–0·42	—	—	—
C.I. (15)	0·74–0·76	0·75	—	—

Female

	Length		Breadth	
	Range	Mean	Range	Mean
Head (27)	0·57–0·65	0·61	0·43–0·49	0·46
Prothorax (10)	—	—	0·29–0·33	0·32
Pterothorax (10)	—	—	0·51–0·54	0·52
Abdomen (10)	1·50–1·60	1·52	0·62–0·69	0·67
Total (10)	2·47–2·57	2·49	—	—
C.I. (27)	0·74–0·79	0·76	—	—

Degeeriella r. subsp.

(from Tendeiro, in press)

	Male (2)		*Female* (5)	
	Length	Breadth	Length	Breadth
Head	0·57–0·58	0·46–0·47	0·61	0·49–0·50
Prothorax	—	0·34	—	—
Pterothorax	—	0·48–0·49	—	—
Abdomen	1·20–1·23	0·55	—	—
Total	2·16–2·18	—	—	—
C.I.	0·81	—	0·80–0·82	—

The phlyctopygus *Species Group*

1–12. As in *fulva* group.
13. Male genitalia of distinctive type ; penial sclerite present.
14. As in *fulva* group.
15. As in *regalis* group.
16. Sternocentral setae of segments III–VI normally more than 4.
17. As in *fulva* group.

This species group, which has only two known species, is distinguished from all other groups by the form of the male genitalia ; in the characters of the chaetotaxy of the abdomen it resembles the *regalis* group.

Degeeriella phlyctopygus (Nitzsch), 1861

Type Host : *Pernis a. apivorus* (Linn.)

(Pl. 8, fig. 1 ; Text-figs. 62, 64–67, 96–98)

Nirmus phlyctopygus Nitzsch, 1861. *In* Giebel, *Z. ges. NatWiss.* **17** : 526. Host : *Pernis apivorus*.

This species (redescribed by Clay, 1957*a*) is distinguished from *D. mookerjeei* the only other species in the species group, by the antennae and the genitalia in the male and by the shape of the head in the female.

MALE. Anterior margin of head slightly concave, inner margin of dorsal marginal carina slightly indented medially ; ventral suture does not reach anterior margin of head. Tergite II only with definite median indentation. Pleural thickening of segments III–VI with well-developed re-entrant heads (Text-fig. 65). The genitalia (Text-fig. 62) are unlike any other known species of *Degeeriella* except those of *D. mookerjeei*.

FEMALE. Terga of IX–XI and genital region as in Text-figs. 96–98.

CHAETOTAXY OF ABDOMEN. Male. Tergocentral setae : II, 5–6 ; III–V, 8 : VI, 7 ; VII, 6 ; VIII, 6–7 ; X, 1–2 each side. Pleural setae : II–III, 0 ; IV–V, 1 each side ; VI–VII, 2 ; VIII, 3 ; IX, 3–5 ; X–XI, 0. Sternocentral : II, 5–6 ; III, 6–7 ; IV–V, 6 ; VI, 5–6. Total number of marginal setae, dorsal and ventral, of last segment (1 specimen) : 13. In the female tergocentral setae : II normally 6, range 5–7 ; III–V normally 8, range 7–8 ; VI range 6–8 ; VII–VIII normally 6, range 5–6 ; X, 2 each side. Pleural setae : II–VIII as in male ; IX normally 3 each side, range 3–5 ; X normally 3, range 2–3. Sternocentral setae : II normally 6, range 4–6 ; III–IV normally 6, range 6–7 ; V normally 6, range 5–6 ; VI range 4–6 ; VII–XI as in Text-fig. 96.

MATERIAL EXAMINED. ♂ neotype and 2 ♂, 12 ♀ from *Pernis a. apivorus* (Linn.) from Scotland, Germany and Italy.

Measurements in mm.

	Length Range	Length Mean	Breadth Range	Breadth Mean
Male				
Head (2)	0·56–0·58	—	0·42–0·45	—
Prothorax (2)	—	—	0·30–0·31	—
Pterothorax (2)	—	—	0·46–0·47	—
Abdomen (1)	1·17	—	0·62	—
Total (1)	2·10	—	—	—
Genitalia (1)	0·42	—	—	—
C.I. (2)	0·76–0·77	—	—	—
Female				
Head (11)	0·59–0·63	0·61	0·44–0·48	0·46
Prothorax (8)	—	—	0·32–0·34	0·33
Pterothorax (8)	—	—	0·49–0·53	0·51
Abdomen (8)	1·23–1·53	1·42	0·62–0·72	0·68
Total (8)	2·22–2·50	2·42	—	—
C.I. (11)	0·74–0·77	0·75	—	—

Degeeriella mookerjeei Clay, 1957

Type Host : *Pernis ptilorhyncus gurneyi* Stresemann

(Pl. 8, fig. 2 ; Text-figs. 7, 63, 68, 69, 99)

Degeeriella mookerjeei Clay, 1957, *Proc. zool. Soc., Calcutta, Mookerjee Memor. Vol.* : 342, pl. 15, figs. 2, 4, text-figs. 1B, C, 2B, 3D, F, 4B. Host : *Pernis ptilorhyncus gurneyi* Stresemann.

The male of this species is at once distinguished from *phlyctopygus* and all other known species of *Degeeriella* by the enlarged antennae ; the species is further distinguished from *phlyctopygus* in the male by the details of the male genitalia, the greater number of marginal setae on the last abdominal segment and the pleural thickening ; and in the female by the shape of the head and the form of the pleural thickening.

MALE. Marginal carina and ventral suture of head as in *phlyctopygus*, shape as in Pl. 8, fig. 2. Antenna with segment I enlarged and III with distal post-axial angle prolonged (Text-fig. 99). The ocular and marginal temporal setae are shorter and finer than in *phlyctopygus*, a reduction which may be correlated with the increased size of the antennae. Tergite II–III as in *phlyctopygus* ; pleural thickening narrower with smaller re-entrant heads (Text-fig. 68). Genitalia similar to those of *phlyctopygus* but differ in detail (Text-fig. 63) ; it should be noted that the sclerite supporting the penis is curved dorsoventrally and therefore when pressed flat on a slide is distorted in various ways. Internal genitalia unlike any other seen, with short broad vesicular apparatus, apparently formed from two single-chambered lobes only and with vasa deferentia entering near base (Text-fig. 7) ; ductus ejaculatorius long and coiled.

FEMALE. Similar to that of *phlyctopygus* but differs in the shape of the head (see Clay, 1957). There do not appear to be any constant characters distinguishing the genital region of the two species ; there is individual variation in the shape of the genital plate, number of setae and a small amount of variation in the shape of the sclerites.

CHAETOTAXY OF ABDOMEN. Tergocentral setae : II normally 6, range 6–7 ; III-V normally 8, range 6–9 ; VI–VIII in the male normally 6, range 6–7, in the female VI–VII normally 6, range 4–9 ; VIII range 3–6 ; X in the male, 1–3 each side and in the female 2 each side. Pleural setae as in *phlyctopygus*. Sternocentral setae : II, 4–7 ; III–VI in the male normally 6, range 4–6, in the female range 5–8 ; VII–VIII in male as in *fulva*, the usual spine-like seta may be elongated in some specimens. Total number of marginal setae on last segment of male varies from 22–29.

NYMPHS. Third instar nymphs have the anterior margin of the head rather similar to that of *D. fulva* but somewhat more pointed.

MATERIAL EXAMINED. ♂ holotype and 20 ♂, 26 ♀ paratypes from *Pernis ptilorhyncus gurneyi*[1] from Thailand and from *P. ptilorhyncus ruficollis* from Nepal ; 8 ♂, 8 ♀ from *Pernis ptilorhyncus* subsp. from Myitkyina, Upper Burma.

[1] The form *gurneyi* is doubtfully distinct from *ruficollis*.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (9)	0·60–0·63	0·62	0·45–0·47 (10)	0·46
Prothorax (6)	—	—	0·33–0·35	0·34
Pterothorax (6)	—	—	0·49–0·52	0·50
Abdomen (6)	1·17–1·29	1·25	0·55–0·62	0·59
Total (6)	2·21–2·37	2·30	—	—
Genitalia (4)	0·47–0·49	0·48	—	—
C.I. (9)	0·73–0·77	0·75	—	—

Female

	Length Range	Length Mean	Breadth Range	Breadth Mean
Head (19)	0·62–0·67	0·63	0·47–0·50	0·48
Prothorax (10)	—	—	0·34–0·37	0·35
Pterothorax (10)	—	—	0·50–0·55	0·53
Abdomen (10)	1·55–1·68	1·60	0·64–0·75	0·68
Total (10)	2·57–2·78	2·67	—	—
C.I. (17)	0·745–0·775	0·755	—	—

The punctifer *Species Group*

1. Head index greater than 0·94.
2. Postantennal dorsal sutures present.
3. Three of the marginal temporal setae each side elongated.
4. Thoracic sternal plate as in Text-fig. 122.
5. Thorax and abdomen with general shape as in Pl. 9, fig. 3.
6. As in *fulva* group.
7. As in *rufa* group.
8. Pleural thickening of segments III–VI without well developed re-entrant heads.
9. Sternal thickening reduced and irregular in shape.
10. Male genital plate as in Text-fig. 103.
11. As in *fulva* group.
12. Female inner genital sclerites fused in mid-line.
13. Male genitalia as in Text-figs. 41, 57 ; penial sclerite present.
14. As in *discocephalus* group.
15. Pleural setae absent on segment II and on X of male.
16. Sternocentral setae of segments III–VI normally more than 4.
17. As in *fulva* group but the last pair of sternal setae are both elongated.

This species group is distinguished from all others by several distinctive characters, see 2, 3, 13 and 15 above ; it has a superficial resemblance to *discocephalus* due to the rounded form of the head and abdomen.

Degeeriella punctifer (Gervais), 1844

Type host : *Gypaëtus barbatus barbatus* (Linn.)

(Pl. 9, fig. 3 ; Text-figs. 8, 41, 57, 83, 103, 108, 122)

Philopterus punctifer Gervais, 1844. *In* Walckenaer's *Hist. nat. Ins.* **3** : 353, pl. 49, f. 1. Host : *Gypaëtus barbatus.*
Nirmus euzonius Nitzsch, 1861. *In* Giebel, *Z. ges. NatWiss.* **17** : 521. Host : *Gypaëtus barbatus.*

Some doubt has been raised about the correct interpretation of *Philopterus punctifer* : Eichler (1941*a* : 179 and 1941*b* : 350) followed Giebel (1874 : 209) and Piaget (1880 : 296) in believing this to be a *Falcolipeurus,* and erected a "neotype" (1941*a* : 179), although without description or figure. However, Neumann (1922 : 235) had already shown that Gervais' figure corresponds with the *Degeeriella* from *Gypaëtus barbatus* and not at all with a *Falcolipeurus.* Neumann is undoubtedly correct ; for although the shape of the head in Gervais' figure of the female is quite unlike the species of *Degeeriella,* the figure is also unlike the description of the head, which is referred to as " disciforme ", which in fact it is ; further, the shape of the head of what is obviously meant to be a *Struthioliperus* on the same plate is also totally unlike that of a *Struthiolipeurus,* so that it must be assumed that Gervais was not able to represent shapes accurately. The dorsal view of the female abdomen and the dorsal and ventral view of the male abdomen represents that of the *Degeeriella* described below.

Male. Head with marginal carina interrupted by ventral suture and only slightly sclerotized at this point dorsally ; narrow but definite hyaline margin present. Mandibles and mandibular supports larger and more strongly sclerotized than in previous species. First marginal temporal seta elongated in addition to the two usual elongated temporal setae. Coni more elongated and more strongly sclerotized than in other species. Postantennal suture present and variable in form ; may be complete and semicircular as in *Lagopoecus* or in the form of two lateral sutures. Thoracic sternal plate as in Text-fig. 122 ; dorsal pterothoracic setae vary from 4–5 each side. Terga II with median unsclerotized area, III narrowed medially. Sternal plates small and irregular, and variable in outline ; genital plate as in Text-fig. 103. Genitalia of distinctive form (Text-figs. 41, 57).

Female. Terga of IX–XI as in Text-fig. 108. Genital region as in Text-fig. 83 ; inner genital sclerites fused in mid-line.

Chaetotaxy of abdomen. Tergocentral setae : II normally 6, range, 5–7 ; III–IV normally 8, range 7–9 ; V range 6–8 ; in the male VI–VII, 6–7, occasionally 4 or 5 ; VIII, 4–7 ; IX, 1–3 each side. In the female VI as in male ; VII normally 4, range 3–7 ; VIII normally 4, range 2–6 ; X, 2 each side. Pleural setae : II, 0 ; III–V, 1 each side ; VI–VII, 2 ; VIII, 3 (occasionally 4) ; IX, 2 ; X in the male, 0 and in the female 2 and occasionally 3 on one side. Sternocentral setae : II–V normally 8, range 5–10 ; VI normally 6, range 6–8. In the male the last pair of sternal setae are both elongated. Total number of marginal setae of last segment of male varies from 10–16.

NYMPHS. First and second instar nymphs have been seen, these resemble the adult in the shape of the head, but the marginal carina is fully sclerotized dorsally.

MATERIAL EXAMINED. Eighteen ♂, 34 ♀ from *Gypaëtus barbatus aureus* (Hablizl) from Afghanistan and Sikkim.

Neotype of *Philopterus punctifer* Gervais : Male, slide no. 20071, in the Meinertzhagen collection, British Museum (Natural History) from *Gypaëtus barbatus aureus* from Sikkim ; 16 ♂, 34 ♀ neoparatypes from the same host form.

Neotype of *Nirmus euzonius* Nitzsch : Male, slide no. 10047, in the Meinertzhagen collection, British Museum (Natural History) from *Gypaëtus barbatus aureus* from Afghanistan.

Measurements in mm.

Male

	Length		Breadth	
	Range	Mean	Range	Mean
Head (14)	0·55–0·60	0·57	0·59–0·65	0·63
Prothorax (10)	—	—	0·33–0·37	0·36
Pterothorax (10)	—	—	0·52–0·57	0·54
Abdomen (10)	1·00–1·13	1·10	0·83–0·95	0·89
Genitalia (1)	0·53	—	—	—
Total (10)	1·82–2·05	1·96	—	—
C.I. (14)	1·05–1·13	1·10	—	—

Female

	Length		Breadth	
	Range	Mean	Range	Mean
Head (23)	0·58–0·67	0·61	0·64–0·73	0·68
Prothorax (10)	—	—	0·35–0·42	0·39
Pterothorax (10)	—	—	0·57–0·65	0·60
Abdomen (10)	1·18–1·48	1·34	—	—
Total (10)	2·08–2·68	2·35	—	—
C.I. (23)	1·09–1·13	1·11	—	—

Degeeriella gypsivorum Eichler, 1943

Type host : *Gyps himalayensis* Hume

Degeeriella gypsivorum Eichler, 1943. *Zool. Anz.* **142** : 93, fig. 2. Host : *Gyps himalayensis Hume.*

There is practically no description of this species : it is said to be somewhat smaller than *punctifer*, but no measurements are given and the preantennal region of the head is said to be parabolic in form, but there is no figure. The figure of the genitalia shows these structures to be similar to those of *punctifer*. Whether this is a good species, a subspecies or a synonym of *punctifer* must wait for an examination of the types or material from the type host.

SPECIES SEDIS INCERTAE

Philopterus aguiae Gervais, 1844

Philopterus (*Nirmus*) *agiae* Gervais, 1844. *In* Walkenaer's *Hist. nat. Ins.* **3** : 350. Host : *Spizaetus melanoleucus* = *Geranoaetus melanoleucus.*

It seems probable that the specimen from which Gervais made his description of *Philopterus aguiae* did not belong to the *Degeeriella.* In the description he states that the head is twice the breadth of the thorax, but in the *Degeeriella* species from *Geranoaetus* the head is not twice the breadth of the prothorax and certainly not of the pterothorax. Monsieur Brin of the Muséum National d'Histoire Naturelle in Paris has kindly told me that there is none of Gervais's type material in that Museum ; and it is most probably no longer in existence. Specimens from *Geranoaetus melanoleucus* are the same as those from *Aquila,* namely *D. fulva.* It does not seem reasonable to replace the established name *fulva* by *aguiae* which doubtfully refers to a *Degeeriella* and which has never been in general use. The name *Philopterus aguiae* Gervais will, therefore, be submitted to the International Commission on Zoological Nomenclature as a *nomen dubium* for inclusion in the Official Index of Rejected and Invalid Specific Names in Zoology. While this is under consideration by the Commission the name *aguiae* should not be used to replace *fulva.*

Nirmus kunzei Giebel, 1874

Nirmus kunzei Giebel, 1874. *Insecta epizoa* : 125. Host : *Falco tinnunculus.*

This species was described from a single female specimen said to have been taken from *Falco tinnunculus* ; according to the original description the specimen was quite different from *rufa.* The type is lost and the original specimen was probably a straggler, and as the species is not identifiable from the description this name should be discarded as a *nomen dubium.*

Nirmus stenorhynchus Giebel, 1874

Nirmus stenorhynchus Giebel, 1874. *Insecta epizoa* : 129. Host : *Milvus aetolius.*

This species said to have come from *Milvus* is not the same as *regalis* and is impossible to identify from the original description. It is presumably a straggler, perhaps not even from one of the Falconiformes and as the type is lost this name will be submitted to the International Commission on Zoological Nomenclature for inclusion in the Official Index on Zoological Names as a *nomen dubium.*

Nirmus secondaria Osborn, 1896

Nirmus secondaria Osborn, 1896. *Bull. U.S. Bur. Ent.* (N.S.) **5** : 227. Host : *Corvus americanus.*

It is not possible to assign this species with certainty to the *Degeeriella* ; if the types are no longer in existence the name should be discarded as a *nomen dubium.*

Degeeriella masumae Ansari, 1955

Degeeriella masumae Ansari, 1955. *Proceedings VIIth Pakistan Sci. Conf.*, Biology : 42. Host : *Falco jugger* Gray.

Degeeriella splendidus Ansari, 1955

Degeeriella splendidus Ansari, 1956. *Proceedings VIIth Pakistan Sci. Conf.*, Biology : 42. Host : *Cerchneis tinnunculus interstinctus* McClell = *Falco tinnunculus interstinctus* Horsfield.

Both *D. masumae* and *D. splendidus* were published twice as sp. n. : once in the reference given above ; and again in *Indian Journ. Entom.* **17** (1955) : 395, 1956, when the name was changed to *splendens*. There are no figures and the descriptions of the male genitalia make it doubtful whether these belong to the genus *Degeeriella* at all.

Key to the Species of *Degeeriella* Parasitic on the Falconiformes

1		Three marginal temporal setae elongated, remainder minute ; postantennal dorsal sutures present. (Head index more than 0·94)	*punctifer*
–		Two marginal temporal setae elongated ; postantennal sutures absent	2
2	(1)	Head index more than 0·94	3
–		Head index less than 0·90	4
3	(2)	Tergocentral setae of segments II–VIII total more than 46 ; shape of head diagnostic (Pl. 9, fig. 1)	*d. discocephalus*
–		Tergocentral setae of segments II–VIII total less than 44 ; shape of head diagnostic (Pl. 9, fig. 2)	*d. aquilarum*
4	(2)	Sternocentral setae of segments III–VI normally 4, never total more than 18	13
–		Sternocentral setae of segments III–VI normally 6 or more, never total less than 20. (Pleural setae present on segment IV)	5
5	(4)	Male without penial sclerite and with pleural setae on segment X ; female genital plate with median posterior prolongation	6
–		Without above characters	7
6	(5)	One seta each side of ventral endomeral arm ; head as in Text-figs. 126–128	*r. carruthi*
–		Two setae each side of ventral endomeral arm ; head as in Pl. 6, fig. 3	*r. rufa*
7	(5)	Males	8
–		Females	12
8	(7)	Anteriorly curved sclerite supporting penis each side (Text-fig. 56)	9
–		Genitalia not as above (Text-figs. 62–63)	11
9	(8)	Shape of dorsal endomeral plate as in Text-fig. 40	*r. deignani*
–		Shape of dorsal endomeral plate as in Text-fig. 39	10
10	(9)	Fused terga of IX–X considerably narrowed and arched medially (Pl. 5, fig. 1)	*r. regalis*
		Fused tega of IX–X not so narrowed and arched medially (Pl. 5, fig. 3)	*r. castanea** *r.* subsp.* (p. 191)
11	(8)	First segment of antenna enlarged, third with distal postaxial angle prolonged	*mookerjeei*
—		Antenna simple	*phlyctopygus*

* Shape of heads of males and females diagnostic, see figures and descriptions.

12 (7) Inner genital sclerites fused or approximated medially (Text-fig. 80) . *r. regalis*
— Inner genital sclerites separated medially . . . . *r. deignani**
*r. castanea**
r. subsp.*
*phlyctopygus**
*mookerjeei**
13 (4) Segment IV with one pleural seta each side (terga II–III indented medially) *hopkinsi*
— Segment IV without pleural seta 14
14 (13) Segment V with one pleural seta each side 20
— Segment V without pleural seta 15
15 (14) Ventral carina with a definite flattened edge enteriorly, to which is attached lobe of pulvinus (Text-fig. 125); inner genital sclerites fused medially . 16
— Not as above 17
16 (15) Penial sclerite not joined to penis; female genital plate with median posterior prolongation . . . . *guimarães i*
— Not as above . . . . *meinertzhageni*
17 (15) Pleural thickening without well developed re-entrant heads . . . *leucopleura*
— Pleural thickening of at least some segments with well developed re-entrant heads 18
18 (17) Head broad and rounded anteriorly, breadth at temples: 0·47–0·52 mm. *africana*
– Head narrower and pointed anteriorly, breadth at temples: 0·36–0·41 mm. . 19
19 (18) Tergal plates apparent on segment XI of male; genitalia diagnostic (Text-figs. 36, 54) . . . . *elani**
— Tergal plates not apparent on segment XI of male; genitalia diagnostic (Text-figs. 37, 53) . . . . *tendeiroi**
20 (14) Ventral carina developed anteriorly each with a flattened inner edge. (Marginal temporal carinae broad; tergite III with at least an anterior concavity) *elbeli*
— Not as above 21
21 (20) Tergite III without definite median indentation 22
— Tergite III with definite median indentation 25
22 (21) Ventral outline of pleural thickening approximately straight 23
— Ventral outline of pleural thickening of at least some segments convex . . 24
23 (21) Ventral suture reaches anterior margin of head; male genitalia diagnostic (Text-figs. 26, 42) . . . . *fulva*
— Ventral suture does not reach anterior margin of head; male genitalia diagnostic (Text-fig. 43) . . . . *beaufacies*
24 (21) Male genitalia diagnostic (Text-fig. 45) . . . . *emersoni*
— Male genitalia diagnostic (Text-fig. 44) . . . . *carrikeri*
— Male genitalia diagnostic (Text-fig. 101) . . . . *rima*
25 (21) Central area of tergite II round median indentation more strongly pigmented. (Shape of head and male genitalia diagnostic) . . . . *fusca*
— Not as above 26
26 (25) Tergocentral setae on segments III–VIII, 4 27
— Tergocentral setae on segments III–VIII, 6 or more 28
27 (26) Head narrow, breadth at temples of males and females: 0·35–0·42 mm. *n. haydocki*
— Head broader, breadth at temples of single female: 0·47 mm. . *n. epustulata*
28 (26) Tergite II with definite median slit . . . . *n. nisus**
*n. vagans**
— Tergite II with at most shallow concavity . . . . *n. frater*

* See footnote on previous page.

HOST-LIST
FALCONIFORMES

Host*	*Degeeriella* species	Species group	Page No.
Suborder CATHARTAE	No *Degeeriella.*		
Suborder FALCONES			
Superfamily SAGITTARIOIDEA	No *Degeeriella.*		
Superfamily FALCONOIDEA			
Family ACCIPITRIDAE			
Subfamily ELANINAE			
×*Elanus caeruleus*	*elani*	*elani*	174
E. notatus	,,	,,	
E. leucurus	,,	,,	
×*Chelictinia riocourii*	*meinertzhageni*	,,	176
Subfamily PERNINAE			
×*Elanoides forficatus*	*guimarãesi*	,,	177
×*Aviceda leuphotes*	*elbeli*	,,	172
×*Pernis apivorus*	*phlyctopygus*	*phlyctopygus*	193
×*Pernis ptilorhynchus*	*mookerjeei*	,,	194
Subfamily MILVINAE			
×*Milvus milvus*, *Milvus migrans*, *Milvus lineatus*	*r. regalis*	*regalis*	186
×*Haliastur indus*	,,	,,	
	×*r. deignani*	,,	190
Subfamily ACCIPITRINAE			
×*Accipiter nisus*, *Accipiter striatus*	*nisus nisus*	*fulva*	155
×*Accipiter gentilis*, *Accipiter cooperii*	*nisus vagans*	,,	157
Accipiter badius, *Accipiter tachiro*, *Accipiter virgatus*	*nisus frater*	,,	158
×*Accipiter minullus*	*nisus haydocki*	,,	160
×*Accipiter bicolor*	*nisus epustulata*	,,	161
Melierax musicus	*fulva* +	,,	149
Melierax metabates	,, +	,,	149
Melierax gabar	?	,,	149
Geranoaetus melanoleucus, *Buteo rufinus*, *Buteo rufofuscus*, *Buteo hemilasius*, *Buteo regalis*	*fulva*	,,	144
Buteo jamaicensis	,,	,,	
	r. regalis	*regalis*	186
Buteo harlani, *Buteo lineatus*, *Buteo buteo*, *Buteo vulpinus*, *Buteo burmanicus*, *Buteo lagopus*	*fulva*	*fulva*	144
Buteo swainsoni	*regalis regalis*	*regalis*	186
Buteo galapagoensis	,, ,,	,,	

* Genera and species from which no *Degeeriella* have been seen are not included.
× Type host, + or subspecies.

Host*	*Degeeriella* species	Species group	Page No.
Parabuteo unicinctus	*emersoni*	*fulva*	154
×*Leucopternis polionota*	*carrikeri*	*fulva*	153
×*Kaupifalco monogrammicus*	*rima*	,,	150
×*Butastur teesa*	*beaufacies*	,,	152
Hypomorphnus urubitinga	?	,,	149
×*Buteogallus gundlachii*	*emersoni*	,,	154
Lophaëtus occipitalis	*fulva*+	,,	149
×*Stephanoaëtus coronatus*	*africana*	,,	151
Polemaëtus bellicosus	*fulva*+	,,	149
Hieraaëtus ayresii	*fulva*+	,,	149
	fulva	,,	144
×*Aquila chrysaëtos*	*discocephalus*	*discocephalus*	170
	aquilarum		
Aquila heliaca	*fulva*	*fulva*	144
	d. aquilarum	*discocephalus*	
Aquila rapax	*fulva*	—	
	d. aquilarum	*discocephalus*	
×*Aquila nipalensis*	,, ,,	,,	
Aquila clanga	*fulva*	*fulva*	
	d. aquilarum	*discocephalus*	
Aquila pomarina	*fulva*	*fulva*	
	d. aquilarum	*discocephalus*	
Aquila verreauxii	*fulva*	*fulva*	
Aquila wahlbergi	,,	,,	
×*Haliaeetus vocifer*	*r. castanea*	*regalis*	190
Haliaeetus pelagicus	*d. discocephalus*	*discocephalus*	168
Haliaeetus leucoryphus	*regalis*+	*regalis*	
Haliaeetus leucocephalus	*d. discocephalus*	*discocephalus*	168
×*Haliaeetus albicilla*	,, ,,	,,	
Icthyophaga ichthyaetus	*fulva*+	*fulva*	149
Subfamily AEGYPIINAE			
×*Gyps himalayensis*	? *gypsivorum*	*punctifer*	197
×*Gypohierax angolensis*	*r.* subsp.	*regalis*	191
×*Gypaëtus barbatus*	*punctifer*	*punctifer*	196
Subfamily CIRCINAE			
Circus cyaneus	*fusca*	*fulva*	162
Circus macrourus	,,	,,	
Circus pygargus	,,	,,	
Circus melanoleucus	,,	,,	
×*Circus aeruginosus*	,,	,,	
Subfamily CIRCAETINAE			
×*Terathopius ecaudatus*	*hopkinsi*	,,	164
Circaëtus gallicus	*leucopleura*	,,	165
Circaëtus gallicus	*leucopleura*	,,	
Circaëtus cinereus	,,	,,	
×*Circaëtus cinerascens*	,,	,,	
Spilornis cheela	?	,,	149
Family FALCONIDAE			
Subfamily POLIHIERACINAE			
Neohierax insignis	? (Host record needs confirmation)	*rufa*	
×*Gampsonyx swainsonii*	*tenderoi*	*elani*	77

Host*	*Degeeriella* species	Species group	Page No.
Subfamily FALCONINAE			
Falco biarmicus	*rufa*	*rufa*	180
Falco cherrug	,,	,,	
Falco mexicanus	,,	,,	
Falco jugger	,,	,,	
Falco rusticolus	,,	,,	
Falco peregrinus	,,	,,	
Falco subbuteo	,,	,,	
Falco cuvierii	,,	,,	
Falco eleonorae	,,	,,	
Falco concolor	,,	,,	
Falco hypoleucos	,,	,,	
Falco fuscocaerulescens	,,	,,	
Falco columbarius	,,	,,	
Falco ardosiaceus	,,	,,	
Falco vespertinus	,,	,,	
Falco amurensis	,,	,,	
Falco naumanni	,,	,,	
×*Falco tinnunculus*	*rufa rufa*	,,	
Falco alopex	*rufa*	,,	
×*Falco sparverius*	*r. carruthi*	,,	185
Ieracidea orientalis	*rufa*	,,	

HOST RELATIONSHIPS

It seems that the relationships of many of the Falconiformes are still the subject of considerable differences of opinion amongst ornithologists (Clay, 1957 : 146), and for this reason any evidence from the distribution of the parasites should be considered. However, as far as *Degeeriella* is concerned much of the evidence is difficult to interpret and only tentative suggestions of the relationship of the hosts can be made. Among the reasons for this are the following : (1) The rather close similarity of most of the species of *Degeeriella,* and the difficulty of judging the significance of the small character differences in relation to the time of separation of the populations and thus of their hosts. (2) The difficulty of knowing which of the species groups are the most primitive. It is not yet possible to describe with any certainty the form of the primitive mallophagen head. The different genera of Ischnocera usually resemble each other in the characters of the anterior margin of the head to a greater extent in the nymph than in the adult and as both nymph and adult live in the same environment, it can be presumed that the head with the complete anterior margin (as found in the majority of nymphs) is the more primitive. It is more difficult to decide whether the primitive Ischnocera had the complete semicircular central carina or the interrupted carina, with the two carinae passing to the anterior margin of the head. In *Degeeriella* the ventral carina is interrupted, but the two carinae are poorly developed anteriorly, except in the *elani* group and the nymphs of *D. rufa.* The nymph of *rufa* also has a dorsal preantennal suture delineating a semicircular dorsal anterior plate. It is not impossible, therefore, that the characters of the head of the *fulva* and *discocephalus* groups are secondary, even secondarily approaching the primitive condition, if the primitive Ischnoceran Mallophaga is presumed to have this type of head. Or alternatively, the species of the *elani* group are derived from a *discocephalus* type, but then it must be postulated that *rufa* shows a more primitive condition of the head in the adult than in the nymph. (3) The difficulty of distinguishing between primary and secondary absences of the species of *Degeeriella.* Was the *discocephalus* type evolved on a common ancestor of *Aquila* and *Haliaeëtus* after this became separated from other hawks? This would suggest a close relationship between these genera. Or did it once have a widespread distribution later becoming extinct except on these hawks? From the resemblance, perhaps of no significance, between the heads of the nymphs of *fulva* and the adults of *discocephalus* it is possible that these species were derived relatively recently from a common ancestor, suggesting an originally wider distribution for *discocephalus.* It is possible that some of the differences between the mallophagan faunas such as those of *Buteo galapagoensis* and *B. swainsoni* and the rest of *Buteo* is due to the extinction of a different member of an original sympatric pair (Clay, 1949 : 296). The *fulva, regalis,* and *discocephalus* types may all have been found on the ancestral Accipitridae and since become extinct on some or other of the present members of the family. However, even this may indicate relationships ; for instance the fact that *fulva* is not found on any of the genera included in the Milvinae suggests that it had already become extinct (if ever present) on an ancestral stock which gave rise to these genera and thus confirms their relationships.

As an indication of the relationships of the Falconiformes as accepted by at least some ornithologists the arrangement in Peters (1931) has been followed. On pp. 202–3 above is a list of hosts (arranged according to Peters) and their known species of *Degeeriella* together with the species groups to which these belong. It can be seen from this list that in general the distribution follows that of the arrangement of their hosts, but with some notable exceptions. The relationships between species of *Degeeriella* which seem to throw some light on the relationships of their hosts are discussed in the following paragraphs.

1. The *Degeeriella* from *Elanus, Chelictinia, Elanoides* and possibly *Aviceda* form a related group, with those from *Chelictinia* and *Elanoides* probably being the most nearly related. The species from *Gamsonyx,* and also possibly *Falco* and *Ieracidea,* all belonging to the family *Falconidae,* should perhaps be included in this group (Clay, 1958 : 2). The *Degeeriella* species from *Pernis* (a genus placed in the Perninae with *Elanoides* and *Aviceda*) are quite distinct and perhaps show affinities with those from the Milvinae.

2. The Milvinae are parasitized by a distinctive species of *Degeeriella* ; the supposition that this may be a relic of a sympatric pair has already been mentioned, and it is therefore possible that the Milvinae are in fact rather more nearly related to the Accipitrinae than their *Degeeriella* suggest.

3. The *Degeeriella* of the Accipitrinae suggest a fairly close relationship between the members of this subfamily, especially between *Aquila* and *Buteo* ; further that there is little difference between this subfamily and the Circinae, and that *Terathopius*

and *Circaëtus* (but not *Spilornis*) of the subfamily Circaetinae are similar but rather more distinct. *Buteo galapagoensis, B. swainsoni, Haliaeetus vocifer* and *H. leucoryphus* have the same species as found on *Milvus* (see above). *Aquila* and *Haliaeëtus* have a second species *discocephalus*, the resemblance of the nymphs of *fulva* to the adults of this species has already been mentioned and perhaps confirms the close relationship of *Buteo* and *Aquila* which is suggested by both being parasitized by *fulva*.

4. Few *Degeeriella* species are known from the Aegypiinae : *Gypaëtus* has a distinctive species (*punctifer*) not closely related to any other except *gypsivorum* from *Gyps himalayensis*. This would suggest that *Gypaëtus* and *Gyps* are wrongly placed between the Accipitrinae and the Circinae. Boetticher & Eichler (1954) considered that the *Degeeriella* species found on *Aquila* and *Gypaetus* showed a relationship between these hosts, but this was based on the erroneous assumption that *discocephalus* and *punctifer* were closely related, but the two species resemble each other only in shape. The *Degeeriella* of *Gypohierax* is a subspecies of *regalis*, rather near that of *Haliaeëtus vocifer*, this suggests if no secondary infestation has taken place, that *Gypohierax* is wrongly placed in the Aegypiinae.

5. It seems doubtful whether the genera included in the Falconidae do in fact, form a related group. As already shown the *Degeeriella* from *Gampsonyx* and possibly also *Neohierax, Falco* and *Ieracidea* show a relationship to those on some of the genera included in the Elaninae and Perninae. The subfamily Polyborinae do not have any species of *Degeeriella sens. str.* but are parasitized by a species of the closely related genus *Acutifrons*. The parasites of *Microhierax* and of *Polihierax*, belonging to the Polihieracinae, do not belong to *Degeeriella* and have been dealt with elsewhere (Clay, 1955).

A detailed study of the other genera of Mallophaga living on the Falconiformes may give some further indications of the relationships of their hosts.

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SUMMARY

The characters and distribution of the *Degeeriella*-complex are discussed. *Degeeriella sens. str.*, as found on the Falconiformes, is described. Variations and artefacts, characters of taxonomic importance and the concept of the subspecies in this group are considered. A systematic survey of all known species is given followed by a key and notes on names of which the correct interpretation is doubtful.

Finally some suggestions are made on possible relationships within the Falconiformes based on the distribution of the Mallophaga.

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